NOAA Technical Report NMFS 12

Soviet-American Cooperative Research on Marine Mammals. Volume 1 - Pinnipeds

Under Project V.6. Marine Mammals,
of the US-USSR Agreement on Cooperation
in the Field of Environmental Protection

Francis H. Fay and Gennadii A. Fedoseev (Editors)

September 1984

LIBRARY
DEC 3 1984
National Marine Fisheries Service
2570 Dole Street
Honolulu, Hawaii

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

NOAA TECHNICAL REPORTS NMFS

The major responsibilities of the National Marine Fisheries Service (NMFS) are to monitor and assess the abundance and geographic distribution of fishery resources, to understand and predict fluctuations in the quantity and distribution of these resources, and to establish levels for optimum use of the resources. NMFS is also charged with the development and implementation of policies for managing national fishing grounds, development and enforcement of domestic fisheries regulations, surveillance of foreign fishing off United States coastal waters, and the development and enforcement of international fishery agreements and policies. NMFS also assists the fishing industry through marketing service and economic analysis programs, and mortgage insurance and vessel construction subsidies. It collects, analyzes, and publishes statistics on various phases of the industry.

The NOAA Technical Report NMFS series was established in 1983 to replace two subcategories of the Technical Reports series: "Special Scientific Report—Fisheries" and "Circular." The series contains the following types of reports: Scientific investigations that document long-term continuing programs of NMFS, intensive scientific reports on studies of restricted scope, papers on applied fishery problems, technical reports of general interest intended to aid conservation and management, reports that review in considerable detail and at a high technical level certain broad areas of research, and technical papers originating in economics studies and from management investigations.

Copies of NOAA Technical Report NMFS are available free in limited numbers to governmental agencies, both Federal and State. They are also available in exchange for other scientific and technical publications in the marine sciences. Individual copies may be obtained from: Publications Services Branch (E/AI 13), National Environmental Satellite, Data, and Information Service, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, 3300 Whitehaven St., Washington, DC 20235.

NMFS Honolulu Library
00000000004693

NOAA Technical Report NMFS 12

Soviet-American Cooperative Research on Marine Mammals. Volume 1 - Pinnipeds

Under Project V.6. Marine Mammals, of the US-USSR Agreement on Cooperation in the Field of Environmental Protection

Francis H. Fay and Gennadii A. Fedoseev (Editors)

September 1984

U.S. DEPARTMENT OF COMMERCE
Malcolm Baldrige, Secretary
National Oceanic and Atmospheric Administration
John V. Byrne, Administrator
National Marine Fisheries Service
William G. Gordon, Assistant Administrator for Fisheries

Library
NOAA, National Marine Fisheries Service
SWFC Honolulu Laboratory F/SWC2
2570 Dole Street
Honolulu, HI 96822-2396

PREFACE

Some 25 to 30 yr ago, when we as students were beginning our respective careers and were developing for the first time our awareness of marine mammals in the waters separating western North America from eastern Asia, we had visions of eventually bridging the communication gap which existed between our two countries at that time. Each of us was anxious to obtain information on the distribution, biology, and ecological relations of "our" seals and walruses on "the other side," beyond our respective political boundaries where we were not permitted to go to study them. We were concerned that the resource management practices on the other side of the Bering and Chukchi Seas, implemented in isolation, on a purely unilateral basis, might endanger the species which we had come to know and were striving to conserve. At once apparent to both of us was the need for free exchange of biological information between our two countries and, ultimately, joint management of our shared resources. In a small way, we and others made some initial efforts to generate that exchange by personal correspondence and through vocal interchange at the annual meetings of the North Pacific Fur Seal Commission. By the enabling Agreement on Cooperation in the Field of Environmental Protection, reached between our two countries in 1972, our earlier visions at last came true. Since that time, within the framework of the Marine Mammal Project under Area V of that Agreement, we and our colleagues have forged a strong bond of professional accord and respect, in an atmosphere of free intercommunication and mutual understanding. The strength and utility of this arrangement from the beginning of our joint research are reflected in the reports contained in this, the first compendium of our work.

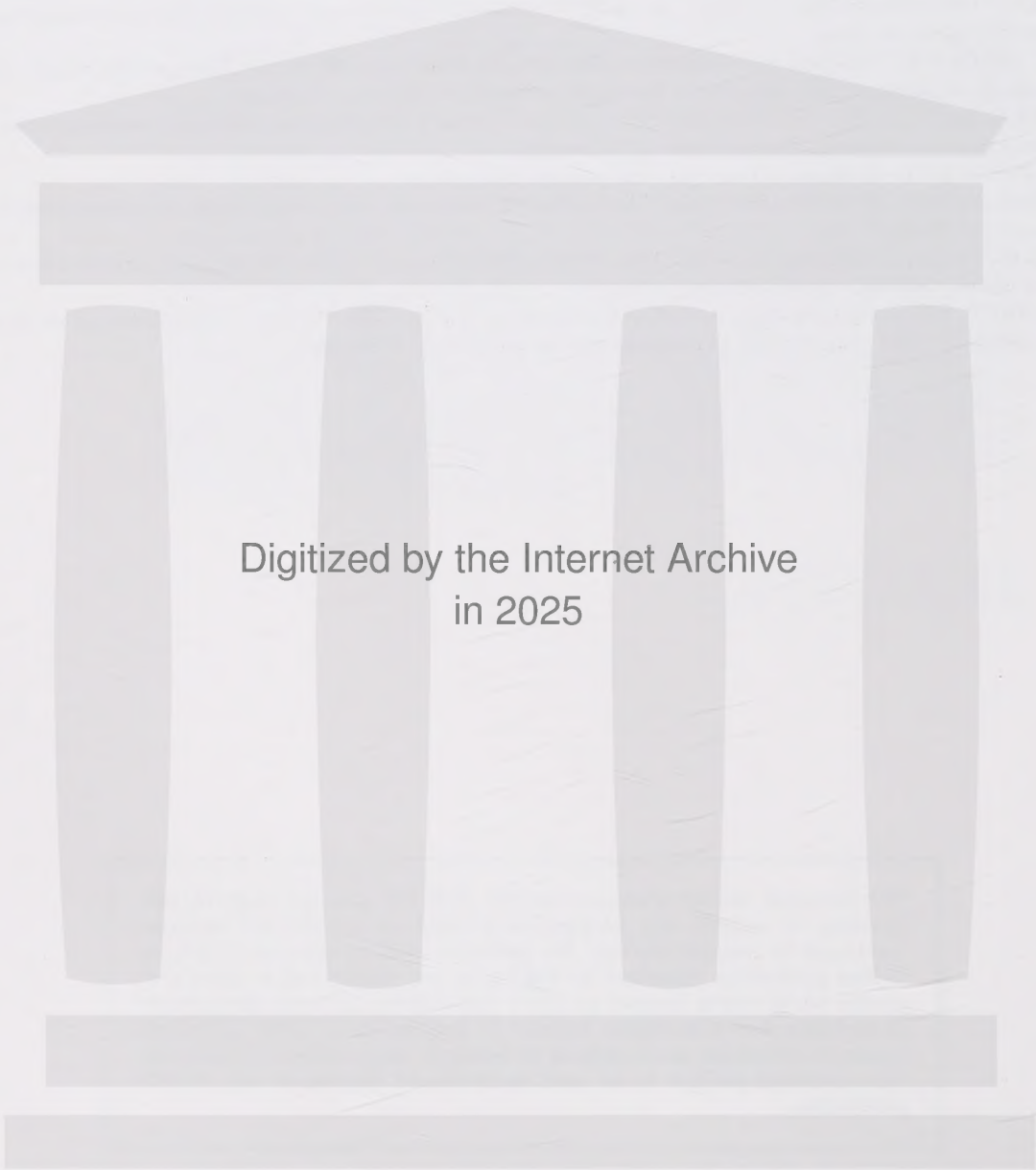
The need for a series of such a compendia became apparent to us in 1976, and its implementation was agreed on by the regular meeting of the Project in La Jolla, Calif., in January 1977. Obviously, the preparation and publication of this first volume has been excessively delayed, in part by continuing political distrust between our governments but mainly by increasing demands placed on the time of the contributors. In this period of growing environmental concern in both countries, we and our colleagues have been totally immersed in other tasks and have experienced great difficulty in drawing together the works presented here. Much of the support for doing so was provided by the State of Alaska, through funding for Organized Research at the University of Alaska-Fairbanks. For its ultimate completion in publishable form we wish to thank Helen Stockholm, Director of Publications, Institute of Marine Science, University of Alaska, and her staff, especially Ruth Hand, and the numerous referees named herein who gave willingly of their time to review each of the manuscripts critically and to provide a high measure of professionalism to the final product.

Francis H. Fay - United States
Gennadii A. Fedoseev - Soviet Union

CONTENTS

MILLER, ROBERT V. The US-USSR marine mammal project 1
BURNS, JOHN J., FRANCIS H. FAY, and GENNADII A. FEDOSEEV. Craniological analysis of harbor and spotted seals of the North Pacific region 5
BURNS, JOHN J., and VITALI N. GOL'TSEV. Comparative biology of harbor seals, *Phoca vitulina* Linnaeus, 1758, of the Commander, Aleutian, and Pribilof Islands 17
BRAHAM, HOWARD W., JOHN J. BURNS, GENNADII A. FEDOSEEV, and BRUCE D. KROGMAN. Habitat partitioning by ice-associated pinnipeds: Distribution and density of seals and walruses in the Bering Sea, April 1976 25
FEDOSEEV, GENNADII A. Use of nonmetrical characters of skulls of Bering Sea seals in a study of the phenotypic structure of their populations 49
BUKHTIYAROV, YURII A., KATHRYN J. FROST, and LLOYD F. LOWRY. New information on foods of the spotted seal, *Phoca largha*, in the Bering Sea in spring 55
DELYAMURE, SEMYON L., MIKHAIL V. YURAKHNO, VALENTIN N. POPOV, LARRY M. SHULTS, and FRANCIS H. FAY. Helminthological comparison of subpopulations of Bering Sea spotted seals, *Phoca largha* Pallas 61
ESTES, JAMES A., and VITALI N. GOL'TSEV. Abundance and distribution of the Pacific walrus, *Odobenus rosmarus divergens*: Results of the first Soviet-American joint aerial survey, autumn 1975 67
DeMASTER, DOUGLAS K. An analysis of a hypothetical population of walruses 77
FAY, FRANCIS H., YURII A. BUKHTIYAROV, SAMUEL W. STOKER, and LARRY M. SHULTS. Foods of the Pacific walrus in winter and spring in the Bering Sea 81
FAY, FRANCIS H., G. CARLETON RAY, and ARKADII A. KIBAL'CHICH. Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger 89
HANSEN, LARRY J., WILLIAM F. PERRIN, ANATOLI S. SOKOLOV, and JAMES G. MEAD. A list of American and Soviet institutions possessing collections of osteological specimens from pinnipeds and sea otters 101

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.



Digitized by the Internet Archive
in 2025

https://archive.org/details/noaa-technical-report-nmfs_1984-09_12

The US-USSR Marine Mammal Project

ROBERT V. MILLER[1]

ABSTRACT

The Marine Mammal Project was organized under Area V (Protection of Nature and the Organization of Preserves) of the US-USSR Agreement on Cooperation in the Field of Environmental Protection. From its inception in 1973, this Project has sponored a wide variety of collaborative research efforts on the biology, ecology, and population dynamics of pinnipeds and cetaceans, principally of the North Pacific region. The earliest activities involved joint and cooperative research on the seals and walruses of the Bering and Chukchi Seas, and those studies are continuing to yield information of substantial value to both countries for conservation and management of shared resources. In conjunction with them, the Project has placed emphasis on development of recommendations for a proposed international agreement on joint management and conservation of those resources. In recent years, the research program has expanded into studies of the husbandry and care of marine mammals in captivity; also implemented were several studies on morphology and taxonomy, which are of prime importance for identification of populational units requiring separate management consideration. The measure of success of such a diverse program is the quantity and quality of reports and publications evolving from it. A number of papers have been published separately, but this is the first compendium of original reports on the studies of Pinnipedia. A second compendium, on studies of Cetacea, is in preparation.

РЕЗЮМЕ

Проект о морских млекопитающих [раздел 05, «Охрана природы и организация заповедников»] создан в 1973 г. в рамках «Соглашения между СССР и США о сотрудничестве в области охраны окружающей среды». Этот проект охватывает разнообразные совместные исследования по биологии, экологии, и динамике популяций ластоногих и китообразных, главным образом в северной части Тихого океана. Первоначальные мероприятия включали совместные исследования по тюленям и моржам Берингова и Чукотского морей; эти работы продолжаются и дают ценную для обоих стран информацию по сохранению и регулированию ресурсов, представляющих большое значение для СССР и США. В этой связи в рамках Проекта первостепенное внимание уделялось разработке рекомендаций для планируемого международного соглашения о совместном регулировании и сохранении этих ресурсов. В последние годы исследовательская программа была расширена и включала изучение китов, а также вопросы разведения и содержания морских млекопитающих в океанариумах. Проводятся также некоторые работы по морфологии и таксономии, которые имеют важное значение для определения отдельных популяций, на которые нужно обратить особое внимание в области регулирования запасов.

Успех данной комплексной программы определяется количеством и качеством докладов и других публикаций, вытекающих из неё. Это - первый сборник таких докладов об исследованиях ластоногих. Второй сборник, посвященный китообразным, готовится к печати.

INTRODUCTION

On 23 May 1972 in Moscow, President Nixon of the USA and President Podgorny of the USSR signed an "Agreement on Cooperation in the Field of Environmental Protection." That agreement recognized the great importance placed by both countries on solving mutual problems of environmental protection, and it expressed the belief that progress could be made on their solution more effectively through cooperative rather than through unilateral action. Among the areas agreed on was cooperation in the "Protection of Nature and the Organization of Preserves." This became Area V of the Environmental Agreement and subsequently included a "Marine Mammal Project" (Table 1).

The objective of our cooperative effort within the Marine Mammal Project has been to develop collaborative research on the biology, ecology, and population dynamics of marine mammals of interest to both countries, thereby contributing to sound management and conservation of those animals. This need for better scientific information, with which to achieve better management of marine mammals, was recognized and enunciated from the beginning.

From that initial step, a vigorous program of cooperative and joint research on marine mammals evolved between our two countries. The first formal meeting between Soviet and American scientists under this program took place in January 1973, during the organizational meeting for development of Area V. In those initial discussions, guidelines were established that have continued to influence our progress. All species of marine mammals were recognized as being of mutual concern, in any geographic area of the world. Nonetheless, the most appropriate areas for concentrated cooperative effort were recognized as those of the North Pacific region, particularly the Bering and Chukchi Seas, because of our common interests and common borders there. A few species, such as northern fur seal and polar bear, were excluded from consideration by the Project, because each already was included under other ongoing international programs.

[1]Deputy Director, National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115, USA.

Table 1.—Organization of activities under the US-USSR Environmental Protection Agreement. The program is administered by the Joint Committee, made up of American and Soviet Chairmen and Executive Secretaries.

Area	Projects
I Prevention of air pollution	1. Conservation of wild species of flora and fauna
II Prevention of water pollution	2. Protection of northern ecosystems
III Prevention of pollution associated with agricultural production	3. Reclamation and revegetation of disturbed land
IV Enhancement of the urban environment	4. Biosphere reserves
V Protection of nature and the organization of preserves	5. Arid ecosystems
VI Protection of the marine environment from pollution	**6. Marine mammals**
VII Biological and genetic effects of environmental pollution	7. Plant and animal ecology
VIII Influence of environmental changes on climate	8. Ichthyology and aquaculture
IX Earthquake prediction	
X Arctic and subarctic ecological systems	
XI Legal and administrative measures for protecting environmental quality	

Generally speaking, the US-USSR Marine Mammal Project consists of four levels of activity:

1) Exchange of published information. In the USA, a full set of exchanged materials is deposited in the library of the National Marine Mammal Laboratory in Seattle, Wash., and duplicates are distributed to institutions involved in the subject research.

2) Continuous exchange of unpublished data resulting from cooperative research efforts. These data are available to both sides and usually are exchanged on a scientist-to-scientist basis.

3) Coordination of research conducted under national programs. This has involved standardization of methods, formats, and scope, and cooperative or joint analysis of resultant data.

4) Joint research expeditions. Scientific personnel of both countries have worked together on joint and complementary research in the field.

The third and fourth levels have been the substantive parts of the Project.

Operationally, the Project involves development of proposals by each side for collaborative work, which are discussed at Project meetings. Those meetings take place at 18-mo intervals, alternately in the USA and the USSR. On the US side, a 7-man Steering/Planning Committee reviews proposals made by scientists throughout the marine mammal research community and assists in developing a coherent package to put forward at the Project meetings. The Steering Committee also makes recommendations on policy and direction of the program. After agreement is reached at the Project level, those proposals are reviewed by the Joint Committee of the overall Environmental Agreement. If approved by that body, they become binding commitments on the two sides.

The following is a resumé of activities of the Project, from its inception in 1973 to the end of its first 6-yr segment in 1978.

PINNIPED RESEARCH

The earliest efforts within the Project involved joint studies of pinnipeds in the Bering and Chukchi Seas. Those studies were initiated because of recognition that unilateral efforts, while contributing to the information base on the biology and ecology of walruses and seals, only addressed part of the problem. Both sides recognized that the populations of walruses, ringed, ribbon, spotted, harbor, and bearded seals occur over wide areas of the Bering and Chukchi Seas, generally corresponding to the movement of the pack ice and transcending political boundaries. The same populations are harvested by both countries, at least for subsistence purposes by native peoples. Therefore, management of those species, to be effective, must be based on understanding and consideration of the total data base, including harvests and other impacting factors from both sides.

A highly successful initial effort was the pinniped research cruise on the RV *Alpha Helix* during July-August 1973. Two Soviet and eight American scientists participated in that cruise, on which studies were conducted of morphology, physiology, taxonomy, and distribution of walruses and several species of seals in the eastern Bering Sea and throughout the Chukchi Sea. Some results from that cruise were reported earlier by Burns and Fay (1974)[3], Halasz et al. (1974), and Hammel et al. (1977). Others are reported in this volume (Burns and Gol'tsev 1984).

In 1974, two American scientists visited several marine mammal laboratories in the Soviet Union to study extensive collections of osteological specimens and to work with Soviet colleagues on the taxonomy of walruses and phocid seals. The data accruing from those studies contributed toward clarification of the taxonomic status of seals of the North Pacific region, as reported by Shaughnessy and Fay (1977) and in the paper by Burns et al. (1984).

During the autumn of 1975, the first cooperative Soviet-American aerial census of walruses was conducted in the Bering and Chukchi Seas. The Soviet surveys covered the regions west of the International Date Line, and the American surveys, the eastern regions. Some of the results and statistical problems associated with the American surveys were reported earlier by Estes and Gilbert (1978); the combined results are reported for the first time in the paper by Estes and Gol'tsev (1984).

In January 1976, a special conference on the biology of walruses and ice-associated seals was held in Moscow. The conference reviewed much of the current state of knowledge of those animals and developed preliminary plans for long-range research, calling for 1) increased emphasis on studies at the community and ecosystem levels, 2) evaluation of current aerial survey methods, and 3) development of joint studies in Alaska and Chukotka on population dynamics, herd structure, and activity patterns. An exchange of information on systems of standard measurements for pinnipeds was discussed at the conference, and consideration of the question of standardization of cetacean measurements was proposed as a subject for discussion at future project meetings. The measurements

[3]Burns, J. J., and F. H. Fay. 1974. New data on taxonomic relationships among North Pacific harbor seals, genus *Phoca* (*sensu stricto*). [Abstr.] Trans. First Int. Theriol. Congr. 1:99. Nauka, Moscow.

used by Soviet and American biologists have not been entirely comparable, but with increasing collaborative efforts, a unified system may eventually be implemented.

Another major item discussed at the conference was the need for a convention for joint Soviet-American conservation of walruses and ice-associated seals in the Bering and Chukchi Seas. Recognizing that unilateral protective measures occasionally may succeed in reversing downward trends of populations, the consensus of the meeting was that closer communication and joint management of these pinnipeds would be of greater mutual value to our two countries. Of particular concern was the potential environmental degradation resulting from increasing human populations and commercial development of the continental shelf. The scientists involved identified a list of basic management and conservation principles that could form the basis for such a convention, and agreed on a proposal to carry this forward in exploratory discussions within their respective governments.

In spring 1976, three American and four Soviet scientists participated in a research cruise on the ZRS *Zagoriany* in the southeastern Bering Sea. New information was obtained on distribution, population structure, and biological characteristics of walruses and of spotted and ribbon seals. Some results of that work were reported by Fay et al. (1977)[4], Gol'tsev (1978)[5], Yurakhno (1978)[6], Fay (1982), and Fay and Furman (1982); others are included in several papers in this volume, for example on helminthology of spotted seals (Delyamure et al. 1984), on time and place of mating by walruses (Fay, Ray, and Kibal'chich 1984), and on feeding habits of walruses (Fay, Bukhtiyarov, Stoker, and Shults 1984) and spotted seals (Bukhtiyarov et al. 1984).

At the same time as the *Zagoriany* expedition in April 1976, three coordinated aerial surveys of pinnipeds in the pack ice of the Bering Sea were conducted by Soviet and American scientists. This was the most thorough coverage of the region ever completed. Some results of the American surveys were reported earlier by Burns and Harbo (1977)[7] and Krogman et al. (1979)[8]. The combined results, reported in this volume by Braham et al. (1984), provide a comprehensive view of distribution and density of walruses and ice-associated seals in the Bering Sea pack ice.

Later in 1976, an American and two Soviet scientists studied ringed and bearded seals at Wainwright, Alaska, and visited several museums in the United States. New concepts of the systematics and biology of those species and of spotted and ribbon seals in the Bering Sea were developed as a result of the visits, some results of which are reported by Fedoseev (1984).

Two cruises, one American and one Soviet, were conducted in the Bering and Chukchi Seas in 1978 with joint scientific participation. Both cruises studied the distribution and biology of walruses and ice seals in their respective areas of deployment, contributing further to the data base on these species and adding to the foundation of knowledge so important to our two nations.

CETACEAN RESEARCH

Studies of cetaceans were initiated within the Project somewhat later than those on pinnipeds. American and Soviet scientists participated jointly in a research expedition aboard the whale-catcher KS *Vnushitelny* from February to April 1975 in the eastern and central tropical Pacific. Activities included "Discovery-marking" and extensive observation of distribution and behavior of large and small cetaceans in a region hitherto little explored by cetologists. Approximately 2,000 large whales were sighted during the cruise and 179 sperm whales were marked. Particularly noteworthy was the sighting of several groups of blue whales between Mexico and the Galapagos Islands and of a group of more than 100 blue whales near the California coast. Also of interest was the finding that sei and Bryde's whales occur together in the same habitat. The data obtained on distribution and behavior of large whales during that cruise, as well as during the *Zharkii* cruise in 1977, are of major significance to the work of the International Whaling Commission. Of especial importance will be the ultimate findings from the Discovery-marking.

More than 6,000 delphinids were sighted during the *Vnushitelny* cruise. They included 10 species of the genera *Stenella, Steno, Tursiops, Peponocephala, Grampus, Orcinus, Lagenodelphis*, and *Globicephala*. The information gained on distribution, herd size, and abundance was of direct value to the American porpoise/tuna program, which is monitoring the status and trends of populations of porpoises in connection with the eastern tropical Pacific yellowfin tuna fishery.

Exchanges of scientists during 1975, 1976, and 1977 enabled collaboration on a series of morphological studies of large and small cetaceans. One study compared the arrangement of blood vessels and muscle weights in the flukes and dorsal fins of several species of delphinids to better define the morphological basis for the hydrodynamic attributes of these animals. Another study compared the ontogeny of two species of delphinids. A major, continuing study is examining the color patterns of several species of large and small cetaceans, primarily sperm and killer whales. The major task of cataloguing the cetacean specimens in Soviet and American museums also was begun during these exchanges.

The scope of cetacean work within the Project has broadened in recent years to include joint participation in field tests of radio-tags remotely applied to humpback whales and cooperative studies of bowhead or Greenland whales. Scientists from both countries are studying the population characteristics and dynamics of Black Sea dolphins and comparing them with those in the eastern tropical Pacific. The information gained from these studies may have significant implications for management programs in both countries.

THE FUTURE

In other areas, joint work is planned or underway on a wide variety of subjects. For example, there is interest in expanding information exchange on husbandry, care, and maintenance of marine mammals in captivity, the plans for which originated during an exchange of scientists who visited oceanaria in both countries in

[4] Fay, F. H., R. A. Dieterich, and L. M. Shults. 1977. Morbidity and mortality of marine mammals - Bering Sea. *In* Environmental assessment of the Alaskan continental shelf. Annual reports of principal investigators for the year ending March 1977, Vol. 1, p. 161-188. NOAA Environ. Res. Lab., Boulder, Colo.

[5] Gol'tsev, V. N. 1978. Materials on reproduction of the Pacific walrus. Abstracts 7th All-Union Conf. Marine Mammals, p. 89. Ministerstvo Rybnogo Khozyaistva SSSR, Moscow.

[6] Yurakhno, M. V. 1978. Toward the study of the helminth fauna of pinnipeds inhabiting the eastern part of the Bering Sea. Abstracts 7th All-Union Conf. Marine Mammals, p. 363-364. Ministerstvo Rybnogo Khozyaistva SSSR, Moscow.

[7] Burns, J. J., and S. J. Harbo, Jr. 1977. An aerial census of spotted seal, *Phoca vitulina largha*, and walruses, *Odobenus rosmarus*, in the ice front of Bering Sea. *In* Environmental assessment of the Alaskan continental shelf. Quarterly reports of principal investigators, April-June 1977, Vol. 1, p. 58-132. NOAA Environ. Res. Lab., Boulder, Colo.

[8] Krogman, B. D., H. W. Braham, R. M. Sonntag, and R. G. Punsly. 1978. Early spring distribution, density, and abundance of the Pacific walrus (*Odobenus rosmarus*) in 1976. Final report, R.U. 14, 47 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

1977 and 1978. American and Soviet scientists are studying the physiology and population dynamics of the Baikal seal, in an effort to gain better understanding of that species. Agreement has been reached to undertake joint studies on the community relationships of sea otters in Alaska and the Commander Islands. New work on walruses, northern sea lions, harbor seals, and ringed seals in Alaska and the Soviet Far East is concentrating on life history, ecology, and population status. Finally, the two governments are continuing exploratory discussions concerning an agreement for mutual conservation of walruses and ice-associated seals in the Bering and Chukchi Seas.

Thus far, the Project has been remarkably successful in implementing exchanges of people and information, but not always smoothly. Major problems have arisen in achieving sufficiently advanced communications regarding cruise schedules, personnel exchanges, travel schedules, visa acquisitions, etc. In this age of almost instantaneous communication by satellite and other sophisticated means, transmission of a single "yes" or "no" between continents sometimes is impossible to arrange in less than a week's time.

A more substantive impact on the joint research has been the restriction of access to key areas of marine mammal concentrations, principally in the Soviet Far East. This problem, which has not yet been solved, has retarded our research efforts on some species, notably walruses, gray whales, and ringed seals. Nonetheless, we are optimistic that options for collaborative work in several desirable locations will emerge, with continuing efforts at both the Project and Joint Committee levels. To fulfill our goals, access to key areas for joint marine mammal research must continue to improve.

At the same time, a lack of effort on some subjects, such as obtaining statistics on subsistence catch of seals, on the part of the United States, causes continued uncertainty in determining the impact of total harvest on the populations of these species.

From a modest beginning, the Project has developed a broad scope of research, which now addresses not only the biology of Bering-Chukchi pinnipeds, but cetacean and pinniped morphology, systematics, and population dynamics, as well as technological exchanges on methods for husbandry and maintenance of marine mammals in captivity. It also has advanced the development of recommendations for international agreement on conservation and management of marine mammal resources of mutual concern to both countries.

The research on pinnipeds thus far has resulted in numerous reports and publications, but this is the first compendium of joint work under the US-USSR Marine Mammal Project. A second volume, on cetacean research, is in preparation for subsequent publication. With further growth of the Project and improvement in communications, we anticipate increasing opportunities for additional collaborative work and publications of this type, to the mutual benefit of our two countries.

LITERATURE CITED

BRAHAM, H. W., J. J. BURNS, G. A. FEDOSEEV, and B. D. KROGMAN.
1984. Habitat partitioning by ice-associated pinnipeds: Distribution and density of seals and walruses in the Bering Sea, April 1976. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:25-47.

BUKHTIYAROV, Y. A., K. J. FROST, and L. F. LOWRY.
1984. New information on foods of the spotted seal, *Phoca largha*, in the Bering Sea in spring. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12: 55-59.

BURNS, J. J., F. H. FAY, and G. A. FEDOSEEV.
1984. Craniological analysis of harbor and spotted seals of the North Pacific region. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:5-16.

BURNS, J. J., and V. N. GOL'TSEV.
1984. Comparative biology of harbor seals, *Phoca vitulina* Linnaeus, 1758, of the Commander, Aleutian, and Pribilof Islands. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:17-24.

DELYAMURE, S. L., M. V. YURAKHNO, V. N. POPOV, L. M. SHULTS, and F. H. FAY.
1984. Helminthological comparison of subpopulations of Bering Sea spotted seals, *Phoca largha* Pallas. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:61-65.

ESTES, J. A., and J. R. GILBERT.
1978. Evaluation of an aerial survey of Pacific walruses (*Odobenus rosmarus divergens*). J. Fish. Res. Board Can. 35:1130-1140.

ESTES, J. A., and V. N. GOL'TSEV.
1984. Abundance and distribution of the Pacific walrus, *Odobenus rosmarus divergens*: Results of the first Soviet-American joint aerial survey, autumn 1975. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:67-76.

FAY, F. H.
1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North Am. Fauna 74, 279 p. U.S. Fish Wildl. Serv., Washington, D.C.

FAY, F. H., Y. A. BUKHTIYAROV, S. W. STOKER, and L. M. SHULTS.
1984. Foods of the Pacific walrus in winter and spring in the Bering Sea. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:81-88.

FAY, F. H., and D. P. FURMAN.
1982. Nasal mites (Acari: Halarachnidae) in the spotted seal, *Phoca largha* Pallas, and other pinnipeds of Alaskan waters. J. Wildl. Dis. 18:63-68.

FAY, F. H., G. C. RAY, and A. A. KIBAL'CHICH.
1984. Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:89-99.

FEDOSEEV, G. A.
1984. Use of nonmetrical characters of skulls of Bering Sea seals in a study of the phenotypic structure of their populations. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:49-54.

HALASZ, N. A., R. ELSNER, R. S. GARVIE, and G. T. GROTKE.
1974. Renal recovery from ischemia: a comparative study of harbor seal and dog kidneys. Am. J. Physiol. 227:1331-1335.

HAMMEL, H. T., R. ELSNER, H. C. HELLER, J. A. MAGGERT, and C. R. BAINTON.
1977. Thermoregulatory responses to altering hypothalamic temperature in the harbor seal. Am. J. Physiol. 232:R18-R26.

SHAUGHNESSY, P. D., and F. H. FAY.
1977. A review of the taxonomy and nomenclature of North Pacific harbour seals. J. Zool. 182:385-419.

Craniological Analysis of Harbor and Spotted Seals of the North Pacific Region

JOHN J. BURNS,[1] FRANCIS H. FAY,[2] and GENNADII A. FEDOSEEV[3]

ABSTRACT

We reexamined the taxonomic status of the *geronimensis, richardsi,* and *stejnegeri* forms of harbor seals, *Phoca vitulina,* in the North Pacific Ocean by comparing the cranial differentiation among them with the differentiation of *P. vitulina* from its sibling species *P. largha,* the spotted seal. This assessment was based primarily on the results of three discriminant analyses and a Q-mode cluster analysis, for which we used both measurements and nonmetrical characters of skulls. The results showed that the differentiation of *vitulina* from *largha* is greater than that among the three Pacific forms of *vitulina.* Within *vitulina,* the *geronimensis* form in southern California and Mexico is not clearly differentiated from *richardsi.* The *stejnegeri* form, conversely, has become differentiated sufficiently for subspecific status. The "boundary" between *stejnegeri* and *richardsi* is not in Near Strait as proposed earlier; instead, it seems to be in the vicinity of the eastern Aleutian Islands and Alaska Peninsula. A firm conclusion on that point cannot be reached, however, without study of additional specimens from that region.

РЕЗЮМЕ

Нами проведён таксономический статус разновидностей обыкновенного тюленя [*Ph. vitulina*] *geronimensis, richardsi* и *stejnegeri* в северной части Тихого океана путем сравнения краниологических различий среди них и сих видом двойником пятнистым тюленем [*Ph. largha*]. Эти исследования основаны главным образом на результатах дискриминантного и клястерного «Q-mode» анализов с использованием метрических и неметрических признаков черепов. Результаты показали, что дифференциация между *vitulina* и *largha* больше, чем среди трёх тихоокеанских разновидностей обыкновенного тюленя [*vitulina*].

Разновидности обыкновенного тюленя *geronimensis* южной Калифорнии и Мексики плохо дифференцированы от *richardsi.* Форма *stejnegeri* напротив дифференцировалась и отвечает статусу подвида.

Самый большой разрыв в градиенте морфологических различий кажется в соседних районах восточной части Алеутских островов и полуострова Аляска.

В заключение отметим, что изложенная точка зрения не может быть окончательной без дополнительных исследований этих подвидов в указанных районах.

INTRODUCTION

A series of recent works on the taxonomy of seals of the genus *Phoca* (in the strict sense) of the North Pacific region by Chapskii (1955, 1960, 1967, 1969), Belkin (1964), Mohr (1965), McLaren (1966), Bigg (1969, 1981), Naito and Nishiwaki (1972, 1975), and Shaughnessy and Fay (1977), has led to worldwide recognition of the sibling species, *P. largha* Pallas, the spotted or larga seal of the seasonal pack ice, and *P. vitulina* Linnaeus, the harbor or common seal of the coasts and islands. The taxonomic status of two other forms, described earlier by Allen (1902) and Doutt (1942) as *P. stejnegeri* of the Commander Islands and eastern Asia and *P. v. geronimensis* of southern California and Mexico, still remains unsettled. The *stejnegeri* form was redescribed by Inukai (1942) as *P. okhotensis kurilensis* and later by Belkin (1964) as *P. insularis.* At present it is regarded as rare and endangered in both Japan and the Soviet Union; for that reason alone, its taxonomic status needs to be resolved.

Shaughnessy and Fay (1977) reviewed the information on harbor and spotted seals of the North Pacific region and concluded (as had Mohr 1965; Chapskii 1969; Bychkov 1971; Burns and Fay 1974;[4] and Kosygin et al. 1975[5]) that the coastal harbor seals of the North Pacific region, from northern Hokkaido in the west to Baja California in the east, appeared to comprise only one polytypic taxon, *P. vitulina richardsi* (Gray), rather than two or three. The concept of a single subspecies of *P. vitulina* in the North Pacific, however, has not been popular. To test that taxonomic theory with somewhat greater rigor than before, we statistically examined both the differences and the similarities among a large series of crania of those seals, collected throughout the North Pacific region. This work, begun in 1970, has been continued since 1973 in the context of the US-USSR Marine Mammal Project.

METHODS

We examined skulls of 435 Pacific harbor and spotted seals, the

[1]Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701, USA.

[2]Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, USA.

[3]Magadan Branch, Pacific Research Institute of Fisheries and Oceanography (MoTINRO), Nagaevskaya 51, Magadan 685013, USSR.

[4]Burns, J. J., and F. H. Fay. 1974. New data on taxonomic relationships among North Pacific harbor seals, genus *Phoca* (sensu stricto). [Abstr.] Trans. First Int. Theriol. Congr. 1:99. Nauka, Moscow.

[5]Kosygin, G. M., A. E. Kuzin, and E. I. Sobolevskii. 1975. Systematic position, morphology, and ecology of the Kuril seal. *In* Marine mammals. Materials 6th all-union conf. 1:151-153. [Abstr.] Naukova Dumka, Kiev.

majority of which were adult animals. These were drawn from 21 of the major osteological collections in the Northern Hemisphere (Appendix I).

For each specimen, insofar as possible, we recorded 37 cranial characters, including 29 measurements and 8 nonmetrical attributes (Figs. 1, 2), in addition to date and location of collection, sex, and relative age. Those characters were selected in part on the basis of universal mammalogical methods and in part on the basis of our mutual experience and our interpretations of Chapskii's (1967, 1969) contributions. Relative age of each specimen was determined from the degree of closure of eight cranial sutures (after Doutt 1942): Occipito-parietal, squamoso-parietal, interparietal, fronto-parietal, interfrontal, basioccipital-basisphenoidal, basisphenoidal-presphenoidal, and intermaxillary. The degree of closure of each suture was assessed visually and assigned a numerical score from 1 to 4. The minimal value of 1 was given for sutures which were open wide; the maximum of 4 was given for those fully ankylosed. Females with total scores of 28 to 32 and males with total scores of 30 to 32 were regarded as adults, usable in the analysis. Skulls with lower scores were not included in the analyses because most of the cranial measurements tend to increase with age during the juvenile and subadult stages of growth.

Each variable was measured to the nearest 0.1 mm; each nonmetrical character was ranked and assigned a numerical score, based on our judgement of its conformity to one of the diagrams in Figure 2. The rank-order of those nonmetric characters is debatable in some

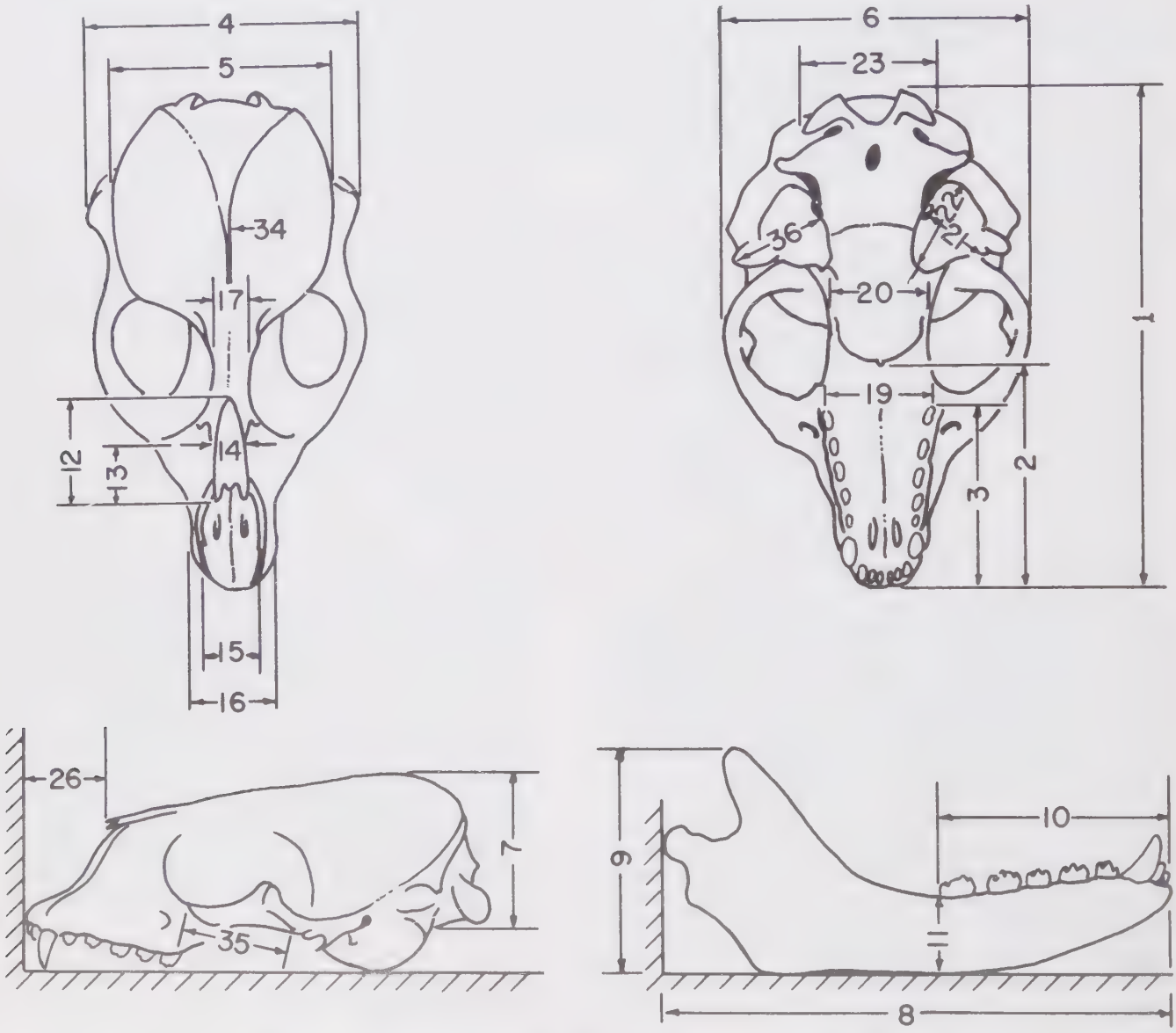


Figure 1.—Dorsal and ventral views of the skull (upper) and lateral views of the skull and mandible (lower) of seals of the *Phoca vitulina-P. largha* type, showing 26 of the measurements used in this study: 1) condylobasal length, 2) palatal length, 3) length of upper tooth row, 4) greatest width at mastoids, 5) greatest width of cranium, 6) greatest zygomatic width, 7) height of cranium, 8) length of mandible, 9) height of mandible at coronoid process, 10) length of lower tooth row, 11) height of mandible behind the molar, 12) overall length of nasals, 13) length of maxillo-frontal suture to anterior end of nasals, 14) width of nasals at maxillo-frontal suture, 15) maximal width of external nares, 16) width of snout at canines, 17) least interorbital width, 19) width of palate behind first molars, 20) least width of palate at pterygoid hamuli, 21) width of bulla from notch anterior to auditory process to middle of carotid foramen, 22) greatest length of bulla, 23) greatest width at condyles, 26) length of snout from anterior edge of nasals, 34) presence of sagittal crest, 35) greatest length of jugal, 36) width of bulla from tip of auditory process to anterior edge of carotid foramen.

instances and obviously not continuous in any. We recognized the weaknesses of combining such discontinuous data with the continuous data from the measured variables, but we did so initially because the emphasis in earlier taxonomy of these seals had been heavily on those categorical attributes. Ultimately, they mostly were not found to be powerful as discriminators.

The skulls of *largha* were from specimens taken in the pack ice of the Okhotsk, Bering, and Chukchi Seas. Those of *vitulina* were from coastal areas in the North Pacific Ocean and southern Bering Sea. Each of those coastal areas was given a numerical code, as shown in Figure 3. Skulls of the three forms of *vitulina* were from specimens taken in the following geographical areas, approximately conforming to the limits originally described by Allen (1902): Areas 100-150 = *stejnegeri*, areas 160-280 = *richardsi*, and areas 300-310 = *geronimensis*.

Males and females were treated separately because of differences in size and proportions, as shown by Fisher (1952), Bishop (1967), Chapskii (1967), Bigg (1969), Naito and Nishiwaki (1972), Burns and Fay (footnote 4), Pitcher and Calkins (1979),[6] and Burns and

[6]Pitcher, K. W., and D. G. Calkins. 1979. Biology of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Final report, R.U. 229, 72 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

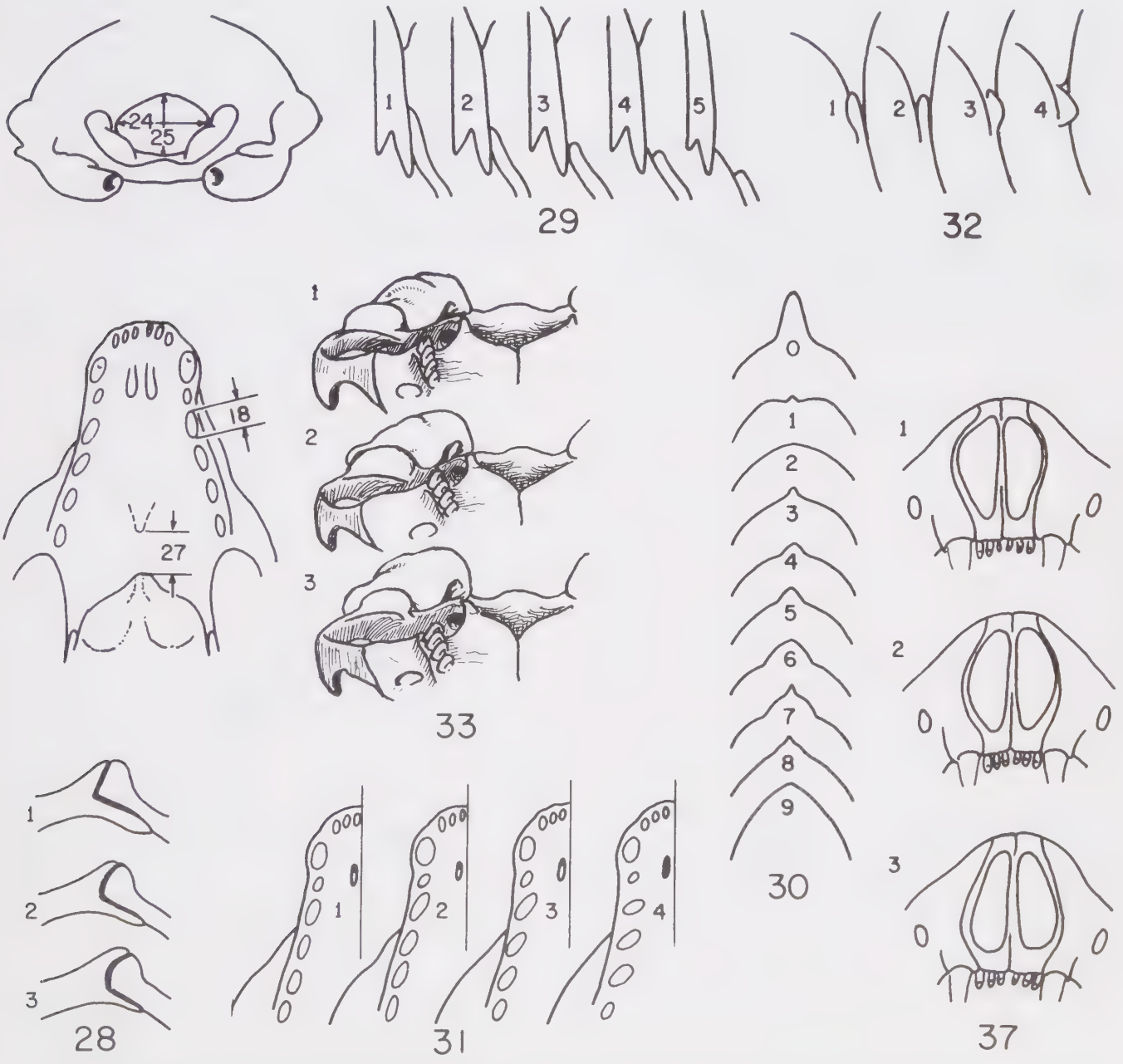


Figure 2.—Cranial measurements and nonmetrical characters in skulls of seals of the *Phoca vitulina-P. largha* type used in this study: 18) greatest anterior-posterior length of second upper premolar, 24) greatest width of foramen magnum, 25) greatest height of foramen magnum, 27) distance from posterior end of vomerine septum to medial edge of palate, 28) shape of jugo-squamosal suture, 29) extent of naso-premaxillary contact, 30) shape of palatal margin, 31) angle of second upper premolar relative to tooth row, 32) shape of pterygoid hamuli, 33) shape of bulla and auditory process in anterior view (skull inverted), 37) shape of anterior nares.

Gol'tsev (1984). Because many of the skulls were partly broken, the full suite of 37 characters was not available from all. For that reason, sample sizes varied among analyses, depending on which of the characters were being compared and the type of statistical treatment employed.

The data were analyzed in four ways. In the first, a set of 11 ratios of cranial dimensions which had been pointed out by Chapskii (1967) as being useful for discrimination between *largha* and *vitulina* were used in a discriminant analysis (Nie et al. 1975). Those ratios were of measurements 2, 3, 4, 12, 13, 22, and 35 relative to condylobasal length, of measurements 6, 16, and 17 relative to greatest width at mastoids, and of measurements 25/24 (see Figs. 1, 2). For that analysis, a sample of 39 specimens of *largha* (21 males (M), 18 females (F)) was compared with 229 specimens of Pacific *vitulina* (87M, 142F).

In the second procedure, we also employed discriminant analysis, but instead of ratios, we used all 37 of the metrical and nonmetrical characters. Our objective was to compare the discrimination between *largha* and *vitulina* with that among the three Pacific forms of *vitulina*. All samples were smaller than in the previous analysis (*largha* 14M, 12F; *stejnegeri* 8M, 12F; *richardsi* 38M, 74F; *geronimensis* 3M, 1F), because of the requirement that each specimen have the full suite of 37 characters.

For our third treatment, we excluded the *largha* phenotype and performed a factor analysis (Nie et al. 1975) of all 37 characters for all of the *vitulina* seals. Resultant factors with an eigenvalue >1.0 were considered. Ten factors for males accounted for 77% of the variance; eight factors for females accounted for 80%. From a varimax rotation, we selected characters with high loadings in the individual factors. For each sex, we chose 14 nonredundant and, as far as possible, nonlinked characters.

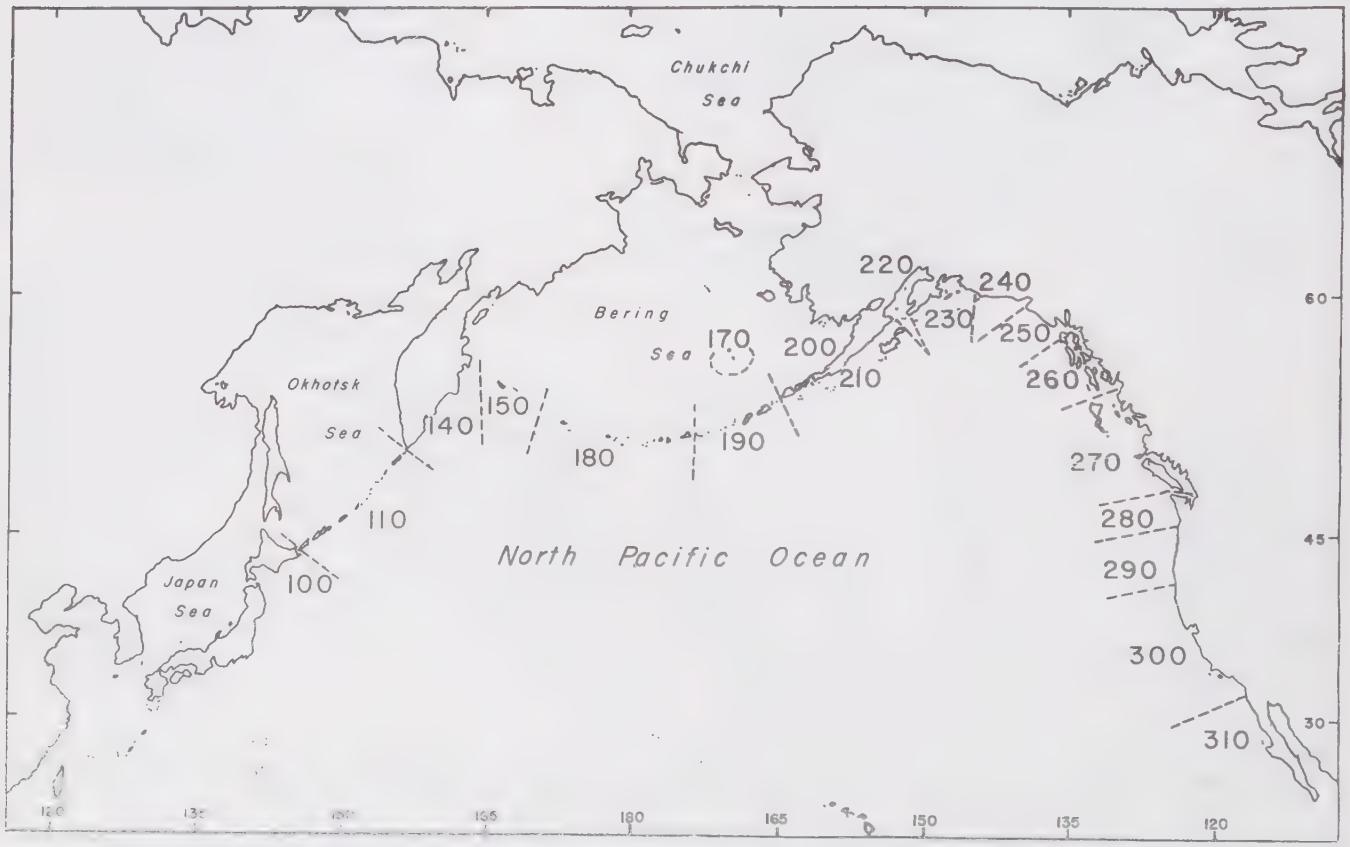
After selecting the 14 characters for each sex, we performed a discriminant analysis with the entire series of *vitulina* samples, subdividing them into five geographical groups, as follows: 100-150 (Hokkaido to Commander Islands), 170-190 (Aleutian and Pribilof Islands), 200-220 (Bristol Bay and Alaska Peninsula to Kodiak Island and Cook Inlet), 230-280 (Prince William Sound to Washington), and 300-310 (California to Mexico). In the discriminant analysis, the objective is to optimize the statistical descriptors of difference among groups; the similarity among groups is not emphasized analytically.

In the final treatment, we performed a Q-mode cluster analysis (Parks 1970), with a simple distance function as a measure of similarity among specimens of the *vitulina* sample. Variables were the 14 selected by factor analysis for males and females. In the Q-mode cluster analysis, distance coefficients were weighted according to percent of total variance accounted for by each principal component. This procedure re-sorts the individual specimens into clusters on the basis of their similarities, rather than differences.

RESULTS

Discriminant Analysis with Measurement Ratios: *vitulina* vs. *largha*

The 11 ratios of cranial dimensions identified by Chapskii (1967) as being useful for discriminating *largha* from *vitulina* were not adequate in themselves to classify correctly all of the specimens.



boundaries (dashed lines) of geographical sampling areas for harbor seals in the North Pacific region. Not shown is code 160, which was assigned to a single specimen from an unspecified locality in "southeastern Bering Sea."

The results of the discriminant analysis were that only 205 (76%) of the 268 skulls were correctly classified on the basis of those 11 ratios; the rest of the specimens were misclassified. Thus, the ratios alone are not as powerful in discrimination as Chapskii had implied, though they clearly have some value.

The discrimination of harbor seals collected in areas bordering the Okhotsk and Bering Seas showed a very strong tendency for greater success (84.5% correct) than did discrimination of harbor seals collected in western North America, from the Gulf of Alaska to Mexico (73.0% correct) (87/103 vs. 92/126, $\chi^2=3.708$: $0.05<P<0.06$). Spotted seals of the Okhotsk Sea also tended to be classified correctly more often than were those of the Bering Sea (Table 1), but the samples were small and the difference between them was not significant ($\chi^2=1.22$, $P>0.25$).

Table 1.—Percent of Pacific harbor, *Phoca vitulina* and spotted, *P. largha*, seal skulls correctly and incorrectly identified by discriminant analysis, based on 11 ratios of cranial measurements.[1]

	Actual taxon			
	largha		*vitulina*	
Predicted taxon	Okhotsk ($N=12$)	Bering ($N=27$)	Eastern ($N=103$)	Western ($N=126$)
largha	83	59	16	27
vitulina	17	41	84	73

[1]Ratios identified by Chapskii (1967) as diagnostic of the *largha* phenotype.

Table 2.—Group means and standard deviations of ratios of skull measurements for male and female spotted and harbor seals.[1]

	P. largha		*P. vitulina*	
Ratio of cranial measurement	Male ($N=21$) mean±SD	Female ($N=18$) mean±SD	Male ($N=87$) mean±SD	Female ($N=142$) mean±SD
2/1:Palatal length/CBL[2]	36.4±18.1	41.2±10.4	38.6±16.3	39.2±14.1
3/1:Length upper tooth row/CBL	27.1±13.5	32.8± 0.8	29.2±12.4	30.7±10.2
4/1.Mastoid width/CBL	45.0±22.4	54.7±13.8	47.5±22.7	51.1±20.2
12/1:Nasal length/CBL	19.1±11.1	23.7± 1.9	20.6± 9.9	21.5± 8.8
13/1:Nasal width from maxillo-frontal suture/ CBL	11.1± 5.7	12.8± 1.4	11.0± 5.4	11.2± 4.7
22/1:Length bulla/CBL	15.1± 7.5	19.0± 0.6	15.7± 7.0	16.6± 6.2
35/1:Length jugal/CBL	21.9±10.9	25.6± 6.5	24.5±10.4	25.0± 9.0
25/24:Height/width foramen magnum	65.1±28.0	72.2±18.6	63.5±31.8	67.8±29.0
6/4:Zygomatic width/ mastoid width	91.0±38.4	97.6±24.8	89.4±41.2	90.3±35.9
16/4:Snout width/mastoid width	28.8±12.3	28.8± 7.5	29.8±13.4	28.7±11.1
17/4:Interorbital width/ mastoid width	8.8± 5.2	10.7± 2.9	10.0± 4.7	9.6± 3.6

[1]All ratios are (A × 100)/B.
[2]CBL = Condylobasal length.

In this analysis, a single discriminant function accounted for all of the discriminating power of the factor matrix for each sex. For males, the eigenvalue of that function was 0.22802; for females, it was 0.13453. Three of the ratios contributed significantly to that function for both sexes (jugal length/ condylobasal length; nasal length from maxillo-frontal suture/condylobasal length; interorbital width/ mastoid width); two contributed nothing (mastoid width/ condylobasal length; length upper tooth row/condylobasal length); each of the other ratios contributed in one sex but not in both. The means and standard deviations of all ratios are shown in Table 2.

Discriminant Analysis—37 Characters: *largha* vs. *vitulina*

With the full suite of 37 metrical and nonmetrical characters, the discriminant analysis correctly distinguished all of the harbor seals from the spotted seals. Within sexes, it also distinguished 98% of the three forms of harbor seals from each other (Table 3). The distinction of the three forms was less effective among sexes; significant overlap developed between *richardsi* and *geronimensis*, though not with *stejnegeri* (Fig. 4). Among the three harbor seal forms, *richardsi* was most similar to *largha*.

For males, two discriminant functions accounted for 90.8% of the relative power to discriminate among the four forms. Within the first function (70.5% relative; eigenvalue 12.35458), the seven variables with the largest standardized coefficients were 10 (length lower tooth row), 27 (length vomerine septum), 16 (width of snout),

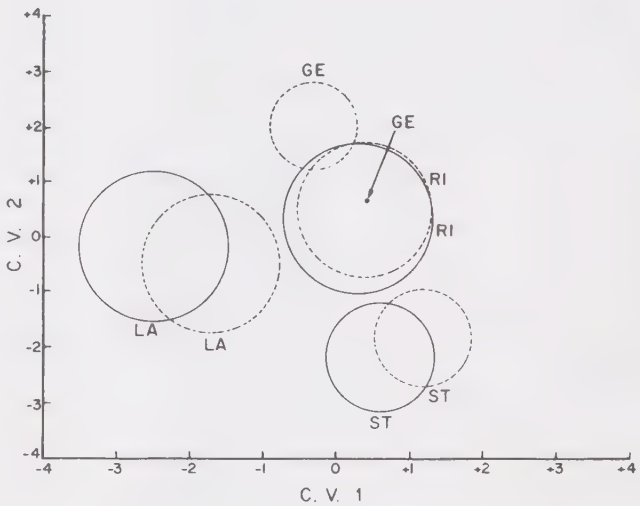


Figure 4.—Distribution of samples of male (dashed circles) and female (solid circles) seals of the *largha* (LA), *geronimensis* (GE), *richardsi* (RI), and *stejnegeri* (ST) forms on the first two canonical variates (CV1 and CV2). Circles enclose 95% of the plotted values for each taxon.

Table 3.—Percent of seal skulls correctly and incorrectly identified to taxon by discriminant analyses, based on 37 cranial characters.

	Actual taxon							
	largha		*richardsi*		*stejnegeri*		*geronimensis*	
Predicted taxon	Male ($N=14$)	Female ($N=12$)	Male ($N=38$)	Female ($N=74$)	Male ($N=8$)	Female ($N=12$)	Male ($N=3$)	Female ($N=1$)
largha	100	100	0	0	0	0	0	0
richardsi	0	0	100	96	0	0	0	0
stejnegeri	0	0	0	4	100	100	0	0
geronimensis	0	0	0	0	0	0	100	100

7 (height of cranium), 8 (length of mandible), 19 (width of palate), and 22 (length of bulla). In the second function (20.3% relative; eigenvalue 3.55208), the three variables with the largest coefficients were 16, 22, and 15 (width of nares).

For females, also, the first two discriminant functions accounted for more than 90% of the relative discriminating power. Within the first function (71.4% relative; eigenvalue 6.45098), the seven most significant characters were 3 (length upper tooth row), 28 (jugo-squamosal suture), 21 (width of bulla), 9 (height at coronoid), 22, 36 (width bulla at auditory process), and 32 (pterygoid hamuli). In the second function (23.0% relative; eigenvalue 2.07899), the three most significant characters were 1 (condylobasal length), 2 (palatal length), and 16.

Factor Analysis: *vitulina* Polytype

In this test, from which *largha* was excluded, the 14 most significant cranial characters were selected for each sex in *vitulina* (Table 4). For the males, these were chosen from six of the first eight discriminant factors, which accounted for 79.5% of the sample variation. For the females, the 14 most significant variables were selected from 9 of the first 10 discriminant factors, which accounted for 77.4% of the sample variation. For both sexes, selection of characters was based on their having the largest coefficients in the varimax rotated factor matrix. Ten of the variables were the same for both sexes; four were specific to each sex.

Table 4.—Principal diagnostic characters selected by factor analysis from the set of 37 metric and nonmetric characters of skulls of Pacific harbor seals.

Sex	Factor	Percent of variation	Principal diagnostic characters[1]
Male	1	45.7	1,2,6,8,9,10,11,16,35 (condylobasal, palatal, mandibular, lower tooth row, and jugal length; zygomatic and snout width; height of mandible at coronoid and behind the molar)
	3	6.0	24 (width of foramen magnum)
	4	4.7	31 (angle of second upper premolar)
	6	4.9	37 (shape of anterior nares)
	7	3.6	29 (extent of premaxillary-nasal contact)
	8	3.1	32 (shape of pterygoid hamuli)
Female	1	40.4	1,2,6,8,9,16 (condylobasal, palatal, and mandibular length; zygomatic and snout width; coronoid height)
	2	8.0	24 (width of foramen magnum)
	3	4.8	14 (width of nasals)
	4	4.4	25 (depth of foramen magnum)
	5	4.1	31 (angle of second upper premolar)
	7	3.3	28 (shape of jugo-squamosal suture)
	8	3.1	32 (shape of pterygoid hamuli)
	9	2.9	22 (length of bulla at auditory process)
	10	2.8	37 (shape of anterior nares)

[1]Refer to Figures 1 and 2.

Discriminant Analysis: *vitulina*— 5 Geographical Groups

Using the 14 variables selected by the factor analysis for each sex, we compared five geographical groups of the *vitulina* samples by discriminant analysis. The geographical boundaries between groups were drawn arbitrarily, mainly with the objective of comparing the variation among regional samples of *richardsi* with that between *richardsi* and the *stejnegeri* and *geronimensis* samples. In effect, group 1 was *stejnegeri* as defined by Allen (1902), groups 2, 3, and 4 were regional samples of *richardsi* from Alaska to Washington, and group 5 included some *richardsi* from California and all (5) of the available *geronimensis*. The sexes were analyzed separately; the results are combined in Table 5. The classification function coefficients for each group are given in Table. 6.

The discrimination among the five groups was moderate to high. About two-thirds to four-fifths of the specimens were correctly placed in their respective geographic groups. The highest proportions of correct placements were at each end of the series: 82% in group 1, 75% in group 5. Of the specimens in group 5, only three (60%) of the *geronimensis* from southern California and Mexico were correctly placed, compared with nine (82%) of the *richardsi* from central and northern California. This difference, however, was not significant ($\chi^2=0.097$, $P>0.25$).

The clinal nature of the morphological variation among geographical groups was shown clearly by this analysis, but a discontinuity in the cline also was indicated. Whereas in most instances

Table 5.—Percent of harbor seal skulls classified to the correct geographical region by discriminant analysis, based on the 14 most diagnostic characters for each sex. Vertical lines connect regional groups with closest affinities.

	Actual region of origin[1]				
Predicted region	100-150 (N=38)	170-190 (N=28)	200-220[2] (N=50)	230-280 (N=47)	300-310 (N=16)
100-150	82	14	0	0	6
170-190	8	71	6	2	0
200-220	3	4	64	17	6
230-280	3	7	22	68	13
300-310	5	4	8	13	75

[1]Refer to Figure 3.

[2]Includes one specimen from "southeastern Bering Sea," for which location was not specified.

Table 6.—Classification function coefficients (Fisher's linear discriminant functions) resulting from discriminant analyses of skulls of male and female *vitulina*, grouped by geographical areas.

		Geographical group[2]				
Sex	Variable[1]	100-150	170-190	200-220[3]	230-280	300-310
Males		(N=16)	(N=13)	(N=11)	(N=20)	(N=9)
	1	0.616	0.608	0.556	0.574	0.596
	2	−0.242	−0.240	−0.171	−0.189	−0.235
	9	−0.293	−0.299	−0.282	−0.295	−0.250
	16	−0.288	−0.267	−0.314	−0.302	−0.323
	24	0.861	0.838	0.844	0.785	0.774
	29	−0.152	−0.025	−0.207	−0.132	−0.090
	31	0.214	0.101	0.188	0.141	0.334
	35	0.409	0.395	0.412	0.376	0.381
	Constant	−700.551	−676.579	−628.634	−604.483	−637.337
Females		(N=22)	(N=15)	(N=39)	(N=27)	(N=7)
	2	0.146	0.164	0.184	0.187	0.194
	14	0.479	0.384	0.365	0.396	0.405
	16	0.240	0.189	0.135	0.126	0.177
	22	1.022	1.045	0.970	0.936	0.875
	24	0.765	0.741	0.691	0.675	0.717
	25	0.593	0.546	0.572	0.556	0.571
	28	0.932	1.014	1.074	0.960	1.034
	31	0.802	0.689	0.664	0.666	0.815
	32	1.092	1.176	1.026	1.012	0.997
	37	−8.823	−7.571	−6.449	−6.576	−7.482
	Constant	−601.158	−575.862	−528.916	−507.420	−531.924

[1]Refer to Figures 1 and 2.

[2]Refer to Figure 3.

[3]Includes one specimen from "southeastern Bering Sea," for which location was not specified further.

affinity between adjacent groups was indicated by about 10 to 20% of incorrect placements, this did not occur between groups 2 and 3. That is, the seals from Hokkaido to the eastern Aleutian Islands appeared to be a craniologically interrelated unit, divergent from the other interrelated unit in the Gulf of Alaska to Mexico. This appeared to confirm Chapskii's (1967, 1969) predictions that the delimitation of *stejnegeri* from *richardsi* would be found at or near the eastern end of the Aleutian Islands.

Cluster Analysis: *vitulina* Polytype

Using the 14 variables identified by the factor analysis for each sex, we submitted *vitulina* to a cluster analysis, which grouped the individual specimens by similarity. For each sex, the specimens tended to be clumped into two primary clusters (I and II), each of which was made up of two secondary clusters (A-B and C-D), as shown in Figures 5 and 6. The compositions of the clusters, in terms of specimens drawn from each of the geographical areas, were similar between sexes but not identical (Table 7).

For the sexes combined, the larger (I) of the primary clusters included 58 (92%) of the specimens from eastern Asia and the Aleutian and Pribilof Islands (areas 100-190), but they also included 17 (71%) of the specimens from the southern coast of the Alaska Peninsula to Kodiak Island (area 210) and 13 (93%) of those from California (area 300). Specimens from the rest of the western coast of North America, between southern Alaska and Washington State, were poorly represented in primary cluster I, but they made up most of primary cluster II for both sexes. Included in cluster II were 38 (79%) of the specimens from localities between Cook Inlet and the coast of Washington (areas 220-280) and both of the specimens from Mexico (area 310); Asian and Aleutian specimens were very poorly represented. The specimens from the Pribilof Islands and Bristol Bay (areas 170, 200) had questionable affiliations. All of the females from the Pribilofs and the males from Bristol Bay were placed in primary cluster I with the Asian-Aleutian group, whereas the one Pribilof male and most of the Bristol Bay females we placed in primary cluster II with the North American group.

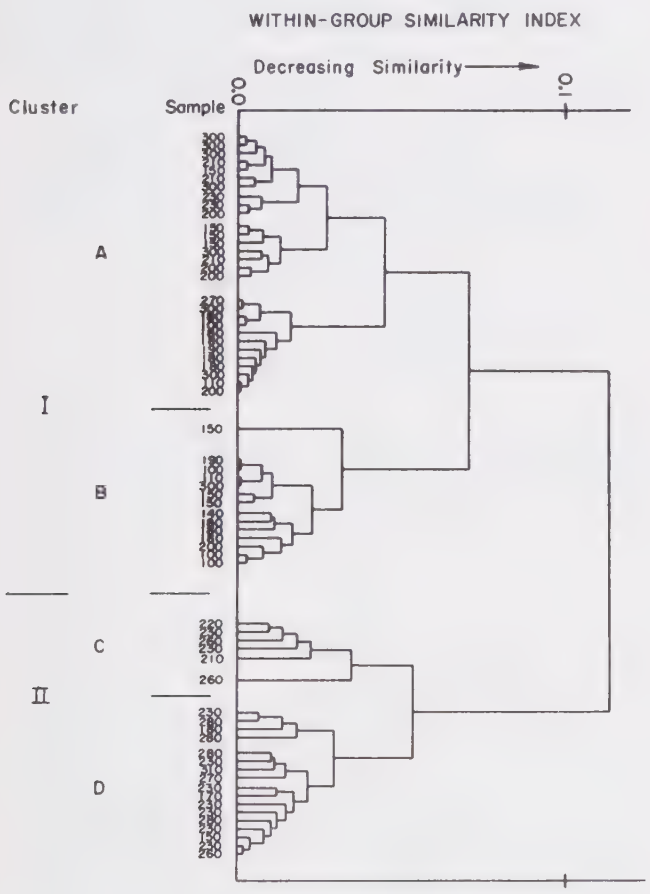


Figure 5.—Dendrogram of results of Q-mode cluster analysis of 66 male seals of the *Phoca vitulina* group in the North Pacific region. The individual specimens making up the primary clusters (I and II) and secondary clusters (A to D) are listed along the vertical axis by the numerical code for the area where they were collected (see Fig. 3).

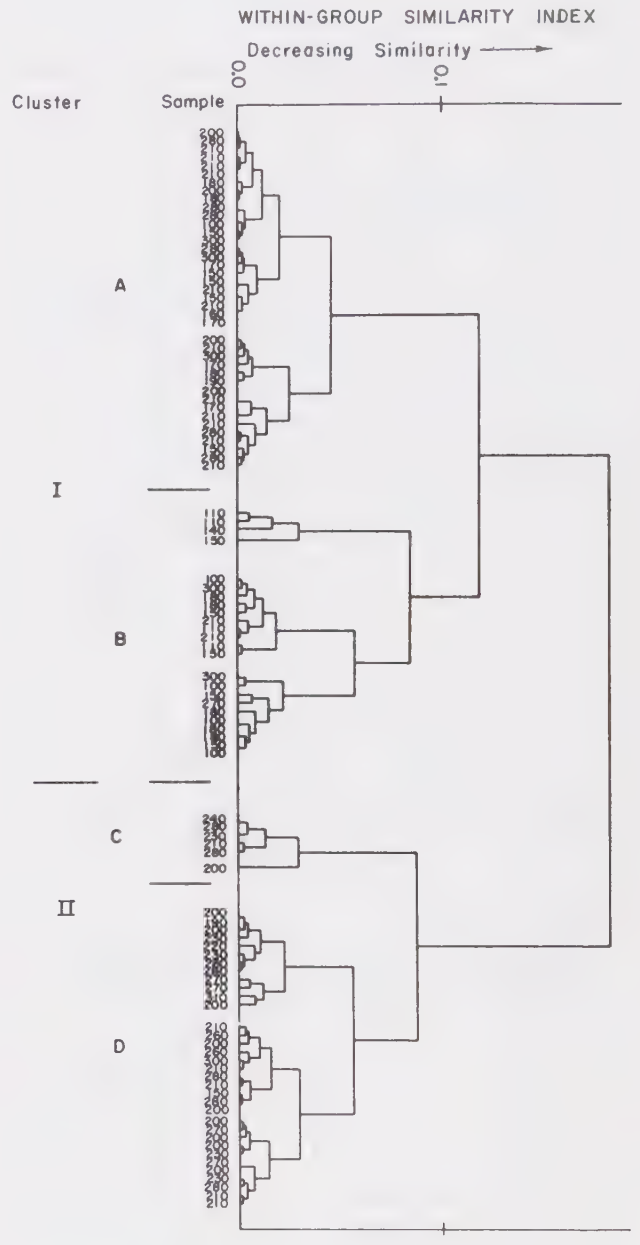


Figure 6.—Dendrogram of results of Q-mode cluster analysis of 104 female seals of the *Phoca vitulina* group in the North Pacific region. The individual specimens making up the primary clusters (I and II) and secondary clusters (A to D) are listed along the vertical axis by the numerical code for the area where they were collected (see Fig. 3).

Table 7.—Numbers of specimens per sex/area making up the two primary clusters of Pacific harbor seals, as indicated by the cluster analysis.

	Primary cluster I		Primary cluster II	
Area[1]	Male	Female	Male	Female
100	4	5	0	0
110	2	4	0	0
140	1	1	0	0
150	7	10	1	1
160	0	1	0	0
170	0	4	1	0
180	8	8	1	0
190	2	1	0	1
200	5	4	0	10
210	3	14	1	6
220	0	0	1	1
230	2	0	9	5
240	0	0	0	1
260	0	0	3	2
270	1	1	1	4
280	0	6	4	7
300	8	5	0	1
310	0	0	1	1

[1]Refer to Figure 3.

In the secondary clusters, the specimens from the coast of Asia (areas 100-140) were placed mainly in cluster B, whereas those from the Commander and Aleutian Islands (areas 150, 180, 190) were about equally distributed in A and B (Table 8). The majority from the Pribilof Islands (area 170), Bristol Bay (area 200), and the Alaska Peninsula-Kodiak area (210) were split about 60/40 between clusters A and D, respectively. The majority of specimens from Cook Inlet to Washington (areas 220-280) were placed in cluster D. A minority of the Alaskan specimens (220-260) was placed in cluster C, and of British Columbia-Washington specimens (270, 280), in cluster A. Accordingly, most of the specimens from California and Mexico (areas 300, 310) were placed in clusters D and A.

These results, like those from the discriminant analyses, further describe the clinal nature of craniological variation within the *vitulina* polytype. They indicate that the Commander-Aleutian seals are most uniform, and that the boundary between the *stejnegeri* and *richardsi* phenotypes definitely is not in Near Strait, as supposed by Allen (1902); neither does it appear to be in the vicinity of Kamchatka Strait. The representation of geographical samples in the clusters suggests that a steepening of the cline between the comparatively stable Aleutian-Asian series and the highly variable North American series takes place between the eastern Aleutian Islands and the Alaska Peninsula. A significant discontinuity in relationships is shown in that area also by the pair-matrix of specimens in the clusters (Fig. 7). Specimens from Asia and the Commander and Aleutian Islands (ACA) were paired in the clusters very significantly more often with specimens from that same region than with those from farther east, on the Pribilof Islands and the North American continent (PNA) (ACA=39/57, PNA=17/113; $\chi^2=46.48$, df=1, $P<0.001$).

Table 8.—Relation of the three forms of Pacific harbor seals (as originally defined) to the composition of the secondary clusters, as indicated by the percent of specimens from the regional samples in each cluster.

			Percent in secondary clusters			
Phenotype[1]	Area code[2]	*N*	A	B	C	D
stejnegeri	100,140	17	18	82	0	0
	150	19	47	42	0	10
richardsi	180,190	21	48	43	0	9
	[3]170,200,210	49	57	6	6	31
	220-260	24	8	0	29	63
	270,280	24	29	4	8	58
	300	11	82	18	0	0
geronimensis	300,310	5	20	20	0	60

[1]As defined by Allen (1902) and Doutt (1942).

[2]Refer to Figure 3.

[3]Includes one specimen from "southeastern Bering Sea," for which the exact locality was not specified.

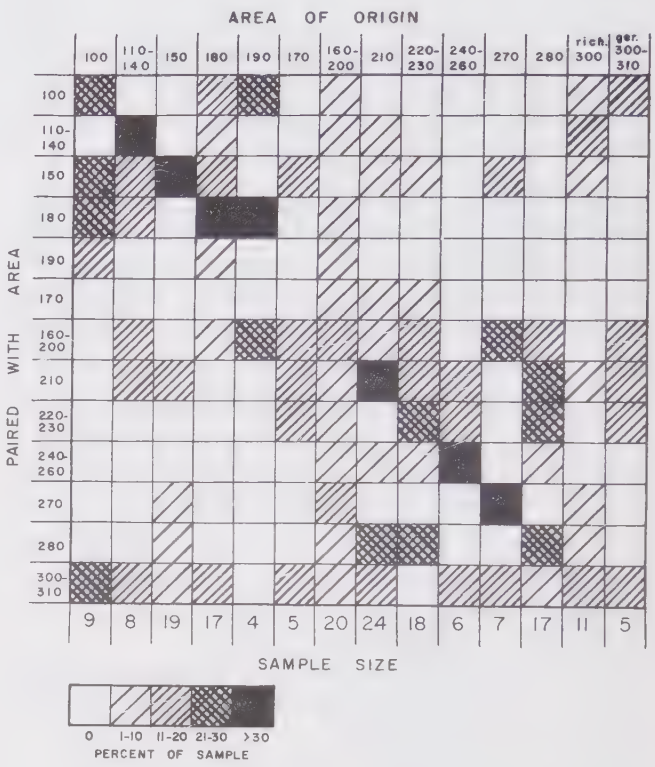


Figure 7.—Pairing frequency matrix from cluster analysis (both sexes) of North Pacific *Phoca vitulina*. Shading indicates comparative percentages of specimens from each geographic sample that were paired (as most similar) with specimens from their own or other localities.

Discriminant Analysis of Secondary Clusters

We performed a discriminant analysis on the four secondary clusters for each sex to identify the characters that contributed the most to their grouping. The most powerful variables in the first function for females were (in descending order of importance) numbers 16 (snout width), 22 (bulla length), 2 (palatal length), and 8 (mandible length); for males, they were 16, 8, 9 (coronoid height), and 35 (jugal length).

The clusters tended to be ordered by size (Table 9). For both the males and the females, the largest skulls were those from the Asian-Commander-western Aleutian seals (cluster B); the smallest (cluster C) were mostly from seals taken in Prince William Sound to southeastern Alaska. A comparable geographical trend in size was shown by Burns and Gol'tsev (1984) for body length.

Table 9.—Means and standard deviations (mm) of the four principal diagnostic variables in the first discriminant function for each sex among the secondary clusters A to D, shown in Figures 5 and 6.

		Secondary clusters			
		A	B	C	D
Sex	Principal character[1]	(N=29M,40F) mean±SD	(N=14M,24F) mean±SD	(N=6M,6F) mean±SD	(N=17M,34F) mean±SD
Male	16	471.5±30.7	531.0±25.8	390.3±14.8	427.8±19.6
	8	1,534.5±51.4	1,624.7±36.1	1,373.5±29.1	1,447.6±44.7
	9	737.4±47.4	793.5±37.4	618.3±19.1	655.0±28.1
	35	658.3±30.7	705.5±23.9	584.5±42.9	610.9±22.4
Female	16	409.8±17.4	446.5±22.4	356.2±15.6	375.5±17.9
	22	399.5±20.6	415.3±21.5	367.0± 9.7	381.2±13.0
	2	935.2±34.3	969.4±33.0	843.3±28.4	883.3±44.3
	8	1,392.2±39.8	1,463.0±44.9	1,271.0±53.5	1,325.9±44.2

[1]Refer to Figures 1 and 2. 16=snout width, 8=length of mandible, 22=length of bulla, 9=coronoid height, 2=palatal length.

DISCUSSION

The harbor or common seals of the North Pacific Ocean were divided by Scheffer (1958) into two taxa, *Phoca vitulina richardsi* of western North America and *P. v. largha* of eastern Asia, essentially following the conclusions of Doutt (1942). Those two taxa were believed to adhere to the coasts and be isolated to some degree from each other in the North Pacific and Bering Sea by the broad expanses of open water in Near and Bering Straits, respectively, where the political boundaries lie between the Soviet Union and Alaska. The anatomical, physiological, and ecological differences between the two forms were not well understood at that time, and the fact that each taxon crossed one of those boundaries and "intruded" into the geographical range of the other was not yet appreciated.

Understanding of the differentiation and geographical distribution of Pacific harbor and spotted seals has been advanced greatly in recent years. We now know that 1) the center of abundance of the spotted seal is in the Okhotsk Sea, whereas that of the Pacific harbor seal is in the Gulf of Alaska, 2) these two taxa are widely sympatric in the southern parts of both the Bering and Okhotsk Seas, even more than was shown by Bigg (1981, fig. 1), and 3) each form maintains its identity clearly in those areas of sympatry. Although both forms haul out at the same time in several of the same locations, even during their respective breeding seasons, they ordinarily do not mix but tend to stay in discrete groups. That they do not interbreed freely is indicated by the scarcity of specimens identifiable as intergrades. Where the two forms coexist in the eastern Bering Sea, parasitological findings also indicate that they are socially and nutritionally divergent (Fay and Furman 1982; Delyamure et al. 1984).

Our analyses of the 11 ratios of cranial measurements selected by Chapskii (1967) for discrimination of harbor from spotted seals showed that *vitulina* tends to be most divergent cranially from *largha* in areas where the two species coexist; it is least divergent where *vitulina* occurs alone. That is, cranial differentiation of Pacific harbor seals from the spotted seals appears to have been enhanced by sympatry. As Shaughnessy and Fay (1977) observed, the same enhancement has taken place in the color of the pelage and in the timing of reproduction and molt.

Thus *P. vitulina* and *P. largha* are now recognizable as sibling species. Superficially, they are very similar and obviously closely related; nevertheless, upon closer inspection they are found to be morphologically, ecologically, socially, and reproductively distinct. Because of their sibling status, their slight craniological differentiation is ideally suited as the standard for comparison with that among the three North Pacific forms of *vitulina* (i.e., *richardsi, stejnegeri,* and *geronimensis*).

Our goal from the outset of this study was to reach a firm, final decision about the taxonomic rank of those three forms. Doutt (1942), Scheffer (1958), Chapskii (1960, 1967, 1969), and Mohr (1965) were unable to weigh enough of the evidence needed to reach such a decision because none of them had access to all of the world's collections. Shaughnessy and Fay's (1977) approach was mainly through review of the literature, but they also had already surveyed most of the world's collections, as well as viewed the living seals in many of the different habitats around the North Pacific. Because of insufficient information, however, they were obliged to take the conservative view in concluding that *geronimensis* was just the southern end of a north-south gradient of increasing frequency of dark pelage in *P. v. richardsi*. Likewise, they conservatively concluded that *stejnegeri* might qualify for subspecific status under *P. vitulina*, but it did not appear to meet the requirements for full specific rank because of extensive primary intergradation with *richardsi*. Our conclusions here are similar.

Our analyses indicated that the cranial differentiation among the three forms of Pacific harbor seals was less than that between *vitulina* and *largha*, and that *richardsi* showed the poorest differentiation from *largha*. The specimens from California and Mexico, which included *geronimensis*, were discriminated well by the 37-character analysis, but the samples were too small (3M, 1F) to give reliable results. Slightly larger samples (9M, 7F) from that region were 75% correctly discriminated in the 14-character analysis of geographic groups, but only five of those specimens (2M, 3F) were from the range described by Allen (1902) for *geronimensis* in southern California and Mexico; the rest were from central and northern California, which is within the described range of *richardsi*.

In the cluster analysis, the five specimens of *geronimensis* were paired with some from Hokkaido, Bristol Bay, Kodiak, Prince William Sound, and California. The specimens of *richardsi* from central and northern California were paired with a similarly broad geographical series. The relationships of both forms were so diverse and so similar that no discreteness was indicated. Hence, we feel that even with larger samples, *geronimensis* probably would not qualify as a subspecies; it appears to be simply the terminal ecomorph in a long, unbroken cline of *richardsi* in western North

America. Certainly, *geronimensis* is much less divergent from *richardsi* than is *stejnegeri*, and the latter's differentiation appears to be of no more than subspecific rank.

The skulls of *stejnegeri* (Commander Islands to Hokkaido) showed differentiation from *richardsi* nearly as great as that between *richardsi* and *largha*, mainly in size. Belkin (1964), McLaren (1966), and Naito and Nishiwaki (1972, 1973) argued for recognition of the large, black seals of the Kuril Islands as a full species, *Phoca insularis* or *P. kurilensis* (=*stejnegeri*), primarily on the basis of marked differentiation from *P. largha* of the Okhotsk Sea. Not necessarily in disagreement but with a broader biogeographical overview, Mohr (1965), Chapskii (1969), Burns and Fay (footnote 4), Kosygin et al. (footnote 5), and Shaughnessy and Fay (1977) responded that the Kuril seal appeared to be conspecific with *P. v. richardsi* and possibly was just the western end of a cline of morphological variation that extends from the Gulf of Alaska to Hokkaido.

The relationship of the Kuril seal to the Pacific harbor seal of western North America is no longer a point of contention, but the degree of that relationship is a question that has not yet been answered to the satisfaction of all parties concerned. In this study, every analysis that we conducted confirmed that the Kuril seal (*stejnegeri*) is well enough differentiated from the harbor seals of western North America (*richardsi*) to qualify for subspecific rank, but in our opinion the requirements for a full species were not met. Although typically large, dark *stejnegeri* of the Kuril Islands may be quite different in appearance from the typically small, pale *richardsi* of Prince William Sound, e.g., they live in similar habitats, behave in similar ways, and both are clearly identifiable as "harbor seals" from their anatomical conformity (in about equal degrees) with *Phoca vitulina* of the North Atlantic Ocean.

The typical *stejnegeri* and *richardsi* are allopatric, but they are not isolated. In the 6,000 km between them is a long series of freely interbreeding populations, in which the diagnostic characters of those two phenotypes vary clinally in degree and/or frequency of occurrence, from the one extreme to the other. Our discriminant analyses appeared to define some sort of "discontinuities" in the cline between the two phenotypes, on the one hand in Near Strait (as assumed by Allen 1902) and on the other in the vicinity of Unimak Pass (as predicted by Chapskii 1967). The discontinuity in Near Strait certainly was not a natural break in the gradient; it was the product of our choice of a potential boundary between *stejnegeri* and *richardsi*, based on Allen's (1902) diagnosis and Shaughnessy and Fay's (1977) assessment of geographic barriers. The other discontinuity, in the vicinity of Unimak Pass, was partly attributable to our grouping of samples, but it was more strongly expressed than any other in the discriminant analyses.

The best indicator of natural discontinuities in the east-west cline was the cluster analysis, because it was not biased by our geographical compartmentalization of the samples. For both sexes, the specimens sorted out into essentially four clusters, which bore some resemblance to the previous geographical groups. More than 90% of the Hokkaido-Kuril-Commander-Aleutian specimens were contained in the first primary cluster; the second primary cluster held about two-thirds of those from the North American coast. Least distinctive were the specimens from the intervening region, the southeastern Bering Sea and Alaska Peninsula, which were almost evenly distributed between the two primary clusters. This intermediacy suggested a point of demarcation between the eastern and western forms in the vicinity of the eastern Aleutians-Alaska Peninsula. A strong discontinuity in that region was indicated also by the makeup of the secondary clusters and was strongly confirmed further by the matrix of paired specimens in the clusters. Because the cline in ratio of color phases also appears to be much steeper in the eastern Aleutians than elsewhere (Shaughnessy and Fay 1977, fig. 3), we suggest that this is the most probable location for a genetic "boundary" between *P. v. stejnegeri* (Allen 1902) and *P. v. richardsi* (Gray 1864), if such a boundary exists.

We are skeptical still about the existence of that boundary, because the present series of specimens is not uniformly representative of seal populations throughout the region. That is, we cannot rule out the possibility that the perceived discontinuity is simply the result of uneven sampling. In these analyses, the specimens from area 180 (western Aleutians) were mostly (16/17) from Amchitka and Adak Islands, some 800 to 1,100 km west of Unalaska Island, where most (3/4) of the specimens for area 190 (eastern Aleutians) were taken. For areas 200 and 210, the samples were principally from Port Heiden (12/19) and Tugidak Island (24/24), respectively, which are about 700 to 800 km east of Unalaska. Thus, the largest samples were from localities 1,500 to 1,900 km apart, and the genetic discontinuity indicated by them may, in actuality, be nonexistant. The whole range of morphologically intermediate forms could be present in that 1,500 to 1,900 km gap. In our opinion, study of many additional specimens from that region will be needed before a firm decision can be reached about the boundary between *richardsi* and *stejnegeri*.

ACKNOWLEDGMENTS

We thank especially the many colleagues and curatorial personnel of the museums and smaller collections who generously made available to us more than half of the specimens used in this study. Many of the rest were collected by us, by K. W. Pitcher of the Alaska Department of Fish and Game, and by other co-workers, with logistic support principally from the Alaska Department of Fish and Game, the United States Coast Guard, the U.S. National Science Foundation, and the Soviet Ministry of Fisheries. We are grateful for advice on statistical procedures received from I. V. Frohne, and from S. J. Harbo, Jr., D. B. Hawkins, A. A. Hoover, I. A. McLaren, and E. H. Miller, who also assisted us by critically reading an earlier draft of this paper. Computer programming services were provided by G. Hanson, L. R. Miller, and J. A. Venable. Our work was sponsored in part (Burns and Fay) by the Alaska Sea Grant Program, the U.S. Marine Mammal Commission, the Alaska Department of Fish and Game, and the University of Alaska, and in part (Fedoseev) by the Soviet Ministry of Fisheries, Pacific Research Institute of Fisheries and Oceanography, Magadan Section.

LITERATURE CITED

ALLEN, J. A.
1902. The hair seals (family Phocidae) of the North Pacific Ocean and Bering Sea. Bull. Am. Mus. Nat. Hist. 16:459-499.

BELKIN, A. N.
1964. A new species of seal from the Kuril Islands—*Phoca insularis* sp. n. Dokl. Akad. Nauk SSSR 158:1217-1220.

BIGG, M. A.
1969. The harbour seal in British Columbia. Fish. Res. Board Can., Bull. 172, 33 p.
1981. Harbour seal *Phoca vitulina* Linnaeus, 1758 and *Phoca largha* Pallas, 1811. *In* S. H. Ridgway and R. J. Harrison (editors), Handbook of marine mammals, Vol. 2 Seals, p. 1-27. Acad. Press, Lond.

BISHOP, R. H.
1967. Reproduction, age determination, and behavior of the harbor seal, *Phoca vitulina* L., in the Gulf of Alaska. M.S. Thesis, Univ. Alaska, Fairbanks, 121 p.

BURNS, J. J., and V. N. GOL'TSEV.
1984. Comparative biology of harbor seals, *Phoca vitulina* Linnaeus, 1758, of the Commander, Aleutian, and Pribilof Islands. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:17-24.

BYCHKOV, V. A.
1971. Review of the status of pinnipeds of the fauna of the USSR. *In* L. K. Shaposhnikov, V. A. Borisov, L. V. Zhirnov, and N. V. Shkarban (editors), Scientific elements of nature conservation, p. 59-74. Ministerstvo Sel'skogo Khozyaistvo, Moscow.

CHAPSKII, K. K.
1955. An attempt at revision of the systematics and diagnostics of seals of the subfamily Phocinae. Tr. Zool. Inst. Akad. Nauk SSSR 17:160-199.
1960. Morphologie systematique, differenciation intra-specifique et phylogenese du sous-genre *Phoca sensu stricto*. Mammalia 24:343-360.
1967. Morpho-taxonomic characteristics of the pagetoda form of the Bering Sea larga. *In* K. K. Chapskii and M. Y. Yakovenko (editors), Investigations of marine mammals, p. 147-176. Polyarnaya Pravda, Murmansk.
1969. Taxonomy of seals of the genus *Phoca sensu stricto* in the light of contemporary craniological data. *In* V. A. Arsen'ev, B. A. Zenkovich, and K. K. Chapskii (editors), Marine mammals, p. 294-304. Nauka, Moscow.

DELYAMURE, S. L., M. V. YURAKHNO, V. N. POPOV, L. M. SHULTS, and F. H. FAY.
1984. Helminthological comparison of subpopulations of Bering Sea spotted seals, *Phoca largha* Pallas. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:61-65.

DOUTT, J. K.
1942. A review of the genus *Phoca*. Ann. Carnegie Mus. 29:61-125.

FAY, F. H., and D. P. FURMAN.
1982. Nasal mites (Acari:Halarachnidae) in the spotted seal, *Phoca largha* Pallas, and other pinnipeds of Alaskan waters. J. Wildl. Dis. 18:63-68.

FISHER, H. D.
1952. The status of the harbour seal in British Columbia, with particular reference to the Skeena River. Fish. Res. Board Can., Bull. 93, 58 p.

INUKAI, T.
1942. Hair seals from the northern waters of Japan. [In Jpn.] Shokubutsu Oyobi Dobutsu 10:927-932, 1025-1030. (Engl. transl., Marine Mammal Div., Northwest Alaska Fish. Cent., Seattle, Wash.)

McLAREN, I. A.
1966. Taxonomy of harbor seals of the western North Pacific and evolution of certain other hair seals. J. Mammal. 47:466-473.

MOHR, E.
1965. Über *Phoca vitulina largha* Pallas, 1811 und weissgeborene Seehunde. Z. Saeugetierkd. 30:273-287.

NAITO, Y., and M. NISHIWAKI.
1972. The growth of two species of the harbour seal in the adjacent waters of Hokkaido. Sci. Rep. Whales Res. Inst. Tokyo 24:127-144.
1973. Kurile harbour seal (*Phoca kurilensis*). *In* Seals: Proceedings of a working meeting of seal specialists on threatened and depleted seals of the world, held under the auspices of the Survival Service Commission of IUCN, p. 44-49. Int. Union Conserv. Nature Nat. Resour. Publ., n.s., Suppl. Pap. 39.
1975. Ecology and morphology of *Phoca vitulina largha* and *Phoca kurilensis* in the southern Sea of Okhotsk and northeast of Hokkaido. *In* K. Ronald and A. W. Mansfield (editors), Biology of the seal, p. 379-386. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, and D. H. BENT.
1975. Statistical package for the social sciences. 2d ed. McGraw-Hill Book Co., N.Y., 675 p.

PARKS, J. M.
1970. Fortran IV program for Q-mode cluster analysis on distance function with printed dendrogram. Kansas Geol. Surv. Computer Contrib. 46, 32 p.

SCHEFFER, V. B.
1958. Seals, sea lions, and walruses; a review of the Pinnipedia. Stanford Univ. Press, Stanford, Calif., 179 p.

SHAUGHNESSY, P. D., and F. H. FAY.
1977. A review of the taxonomy and nomenclature of North Pacific harbour seals. J. Zool. (Lond.) 182:385-419.

APPENDIX I

Sources and Acquisition Numbers of Harbor and Spotted Seal Specimens Used in These Analyses

Harbor Seals

Alaska Department of Fish and Game (ADF&G), Anchorage and Fairbanks, Alaska, USA. (The transfer of specimens to the Geist Museum, University of Alaska, Fairbanks, is in progress.)

Males: 66-20, S-00, S-33, B-4, B-5, B-41, PWS-73-3, PWS-16-75, PWS-19-75, PWS-26-75, PWS-32-75, PWS-76-75, PWS-78-75, PWS-82-75, PWS-107-75, 12-6-65, AH-17-72, AH-10-73, AH-39-73, AH-52-73, AH-56-73, AH-9-74, AH-9a-74, JNO-2-72, JNO-12-72, JNO-13-72, JNO-18-72, JNO-19-72, HS-72-1, HS-72-3, HS-72-6, HS-72-15, N-7-68, CR-3-75, CR-23-75.

Females: 66-12, 66-21, 66-22, 66-23, 66-25, 66-29, 66-30, 66-31, 66-34, 66-39, A-7, A-26, A-27, A-34, A-36, B-1, B-12, B-15, B-16, B-17, B-18, B-27, B-28, B-29, B-30, B-32, B-35, B-37, B-39, PWS-73-13, PWS-73-15, PWS-14-75, PWS-85-75, AH-6-68, AH-21-72, AH-2-73, AH-11-73, AH-23-73, AH-28-73, AH-33-73, AH-35-73, AH-36-73, TU-1-71, TU-2-71, HS-72-4, HS-72-5, JNO-1-68, JNO-20-72, AMC-1-69, N-10-68, CR-2-75, NAN-4-73, KSK-27-73, ADF&G-1, 019, 020, 100, 101, 102, 103, 104, 105, 106.

All-Union Research Institute of Fisheries and Oceanography (VNIRO), Moscow, USSR.

Females: 3484, 29112.

Black Douglas Mammal Collection (BDM), National Marine Fisheries Service, National Marine Mammal Laboratory, Seattle, Wash., USA.

Females: BDM-1272.

California Academy of Science (CAS), San Francisco, USA.

Males: 5, 411, 413.

Females: 527, 530, 15934.

Carnegie Museum (CMP), Pittsburgh, Pa., USA.

Female: 18738.

Fisheries Research Board of Canada (FRBC), Arctic Biological Station, Ste. Anne de Bellevue, Quebec, Canada.

Male: HS8.

Geist Museum, University of Alaska (GMUA), Fairbanks, USA.

Males: 3409, 7265, 7304.

Females: 3702, 7264.

Los Angeles County Museum (LACM), California, USA.

Females: 9539.

Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Mass., USA.

Male: 6157.

Female: 11455.

Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, USA.

Males: 101090, 114778, 140849, REJ-439.

Females: REJ-454, REJ-681.

National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., USA.

Males: 81515, 140401, 140402, 140403, 146430, 146432, 147700, 253045, 273532, 274152, 274155, 275176.

Females: 81517, 81518, 146433, 146434, 147680, 219868, 219873, 219874, 245915, 250712, 250713, 253042, 253043, 253046, 261781, 274146, 276362, 276365.

Ocean Research Institute (ORI), University of Tokyo, Japan.

Males: 69-6, 70-186, 70-208, 70-223, 70-228.

Females: 69-NE3, 70-13, 70-20, 70-35, 70-155, 70-168, 70-187, 70-222.

Pacific Research Institute of Fisheries and Oceanography (TINRO), Magadan, USSR.

Males: 57-1964, 80-1964, 26-1975, 33-1975, 34-1975, 35-1975, 39-1975, 47-1975.

Females: 225, 389, 1-1964, 27-1964, 43-1964, 83-1964, 86-1964, 3-1975, 10-1975, 11-1975, 13-1975, 14-1975, 18-1975, 20-1975, 24-1975, 27-1975, 28-1975, 29-1975, 40-1975, 45-1975, 46-1975.

Puget Sound Museum of Natural History, University of Puget Sound (UPSMNH), Tacoma, Wash., USA.

Males: 15182, 16040, 16043, 16103, 16430.

Females: 15211, 15274, 16039, 16041, 16044, 16054, 16096.

Dr. Robert L. Rausch (RLR), University of Washington, Seattle, USA.

Male: 39716.

Females: 39715, R11332.

Charles A. Repenning, United States Geological Survey, Menlo Park, Calif., USA.

Male: 6842.

Santa Barbara Museum of Natural History (SBMNH), California, USA.

Females: 251, 258, 1895.

University of Arizona (UAZ), Tucson, USA.

Males: 01, 22799.

Vertebrate Museum, University of British Columbia (VMUBC), Vancouver, Canada.

Males: 1470, 7339.

Females: 2159, 2167, 2168, 9530, 9539, 9540, 9541.

Zoological Institute, Academy of Sciences (ZIAS), Leningrad, USSR.

Males: 835, 2679, 26977.

Zoological Museum, University of Moscow (ZMUM), USSR.

Male: 45050.

Spotted Seals

ADF&G

Males: D-55-65, N-10-66, N-30-67, D-191-67, AH-63-73, AH-1-74, AH-2-74.

Females: N-12-66, N-17-66, N-51-67, G-9-69, N-26-72, AH-27-72, AH-28-72, NAN-3-73.

CMP

Male: DC-1586.

FRBC.

Female: PV-410.

GMUA.

Male: 1529.

ORI.

Males: 69-42, 69-49, 70-69, 70-107.

Females: 70-50, 70-56, 70-58.

TINRO.

Females: 7-1975, 41-1975.

USNM.

Males: 219885, 290655.

Females: 219865, 290653.

ZIAS.

Males: 3487, 3491, 29117.

ZMUM.

Males: 10095, 45024, 69371.

Females: 29925, 45025.

Comparative Biology of Harbor Seals, *Phoca vitulina* Linnaeus, 1758, of the Commander, Aleutian, and Pribilof Islands

JOHN J. BURNS[1] and VITALI N. GOL'TSEV[2]

ABSTRACT

Harbor seals, *Phoca vitulina*, of the Aleutian Ridge and Pribilof Islands were studied through field observation and examination of animals (173 seals, 15 fetuses) collected in four areas: The Commander, western Aleutian, eastern Aleutian, and Pribilof Islands. Spotted seals, *Phoca largha*, were not analyzed in this study. Habitats were similar in these four areas and seals were present at all locations visited. Differences in pelage coloration between seals of the Aleutian and Commander Islands were not significant, but there was a trend toward more dark colored seals in the western islands. Growth in relation to age of seals from the four areas was similar, as was fetal growth. Mating was found to occur in July to early August, implantation in November, birth in early June to mid-July, and weaning of pups by mid-August. Some females (33%) first ovulated at age 3. First pregnancy also occurred in some 3-yr-olds; all females had been or were pregnant by age 6. The incidence of pregnancy in sexually mature animals was 75%. Similarities among seals of the Aleutian Ridge include timing of events in the reproductive cycle, size/age relationships including fetal growth, food habits, and habitat utilization. Harbor seals of the North Pacific region vary in size and coloration in an apparently clinal manner over their linearly continuous range from Mexico to Japan.

РЕЗЮМЕ

Изучение обыкновенных тюленей на Алеутско-Командорской гряде островах Прибылова проводилось в полевых условиях и на основе материала полученного от 173 тюленей и 15 эмбрионов, добытых в 4 районах: на Командорских островах, в заподной и восточной частях Алеутских островов, и на Прибыловских островах. Ларга, *Phoca largha* не включалась в это исследование. Среда обитания сходна во всех 4 районах, и тюлени отмечались в каждом из них. Разницы в окраске меха между тюленями Алеутских и Командорских островов не значительна. Однако тюлени с тёмной окраской встречались чаще в западных районах, чем на восточных островах. Рост тюленей с возрастом в каждом из 4 районов был сходным как и утробное развитие. Спаривание происходило с июля до начала августа, прикрепление бластоциста отмечено в ноябре, деторождение протекает с начала июня до середины июля и щенки выкармливаются грудью до середины августа. Самки 33% начинают овулировать в возрасте 3 лет, некоторые трёх-летние тюлени имели первую беременность. Все самки 6-летнего возраста и старше были половозрелы. Число беременных у взрослых животных составляло 75%. Сходство среди тюленей Алеутско-Командорской гряды проявляется в репродукционном цикле, в размерно-возрастном составе развитии эмбрионов, питании и естественной среде обитания. Обыкновенные тюлени северной части тихого океана в пределах непрерывного распространения от Мексики до Японии имеют клинальную изменчивость в размерах тела и окраске.

INTRODUCTION

In an evaluation of the taxonomy and nomenclature of North Pacific harbor seals, Shaughnessy and Fay (1977) reviewed the three taxa recognized at that time: 1) The ice-associated "spotted" or "larga" seal, *Phoca largha* Pallas 1811, of the Bering, Chukchi, Okhotsk, Japan, and Yellow Seas; 2) the eastern Pacific harbor seal, *P. vitulina richardsi* (Gray 1864), distributed from northwestern Mexico to the Gulf of Alaska and westward through the Aleutian and Pribilof Islands; and 3) the western Pacific harbor seal or insular seal, *P. v. stejnegeri* (Allen 1902), of northern Japan (Hokkaido), eastern Kamchatka, and the Kuril and Commander Islands.

Spotted seals are sympatric with harbor seals about eastern Hokkaido (Inukai 1942; Naito and Nishiwaki 1972; Naito 1974, 1976), the Kuril Islands, eastern Kamchatka, and the Commander Islands (Belkin 1964; Marakov 1967; Voronov 1974; Kosygin et al. 1975a,[3] 1975b;[4] Heptner et al. 1976). They are sympatric also in the southeastern Bering Sea from the estuary of the Kuskokwim River south to the Alaska Peninsula, the Pribilof Islands, and, to a limited extent, the eastern Aleutian Islands (Burns 1970; Burns and Fay 1974;[5] Shaughnessy and Fay 1977; Burns and Fay unpubl. data).

There is evidence based on skull characteristics of some intergradation between *largha* and *stejnegeri* in the Okhotsk Sea and between *largha* and *richardsi* in the southeastern Bering Sea (Burns

[1]Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701, USA.

[2]Magadan Branch, Pacific Research Institute of Fisheries and Oceanography (MoTINRO), Nagaevskaya 51, Magadan 685013, USSR.

[3]Kosygin, G. M., A. E. Kuzin, and E. I. Sobolevskii. 1975. Systematic position, morphology, and ecology of the Kuril seal. *In* Marine mammals. Materials 6th all-union conf. 1:151-153. [Abstr.] Naukova Dumka, Kiev.

[4]Kosygin, G. M., A. E. Kuzin, and V. A. Petrova. 1975. The larga of the Kuril Islands. *In* Marine mammals. Materials 6th all-union conf. 1:149-151. [Abstr.] Naukova Dumka, Kiev.

[5]Burns, J. J., and F. H. Fay. 1974. New data on taxonomic relationships among North Pacific harbor seals, genus *Phoca* (sensu stricto). [Abstr.] Trans. First Int. Theriol. Congr. 1:99. Nauka, Moscow.

and Fay unpubl. data). Nevertheless, spotted seals are for the most part clearly differentiated morphologically, physiologically, and ecologically from those two forms (Chapskii 1960, 1967, 1969, 1975;[6] Mohr 1965; Burns 1970; Burns and Fay footnote 5, unpubl. data). Shaughnessy and Fay (1977) concluded that the larga phenotype should be regarded as a separate species, *Phoca largha* Pallas, 1811, as proposed by Chapskii (1967). For that reason, spotted seals have been excluded from the present analysis.

The validity of subspecific distinction for the *richardsi* and *stejnegeri* phenotypes is in question. Their range is linearly continuous along the shores of all suitable land masses around the North Pacific Ocean, from northern Mexico to northern Japan. In the area of their presumed discontinuity, the Aleutian-Commander Ridge, harbor seals occur on all of the islands. The respective ranges of *stejnegeri* and *richardsi* in that area have not been clearly defined. Some authors have included the Aleutian and Pribilof Islands within the range of *stejnegeri* (Chapskii 1967; Belkin et al. 1969; Heptner et al. 1976); others have included those islands within the range of *richardsi* (Burns and Fay 1973; Shaughnessy and Fay 1977). As pointed out by Shaughnessy and Fay (1977), a real possibility exists that the two subspecies comprise a single, trans-Pacific cline as suggested also by Mohr (1965), Chapskii (1969), Bychkov (1971), Burns and Fay (footnote 5), and Kosygin et al. (footnote 3).

In this paper we compare the physical and biological characteristics of harbor seals from the Commander and Aleutian Islands. Data from a few seals taken on the Pribilof Islands are compared as well.

THE STUDY AREA

The Commander and Aleutian Islands are physiographically similar, comprising the emergent portions of the Aleutian Ridge (Fig. 1). According to Wahrhaftig (1965:33): "The Aleutian Islands are a chain of islands surmounting the crest of a submarine ridge 1,400 miles long, 20-60 miles wide, and 12,000 feet high above the sea floor on either side. An arcuate line of 57 volcanoes of Quarternary age, 27 reported active, rises 2,000-9,000 feet above sea level along the north side of the Aleutian Islands. Other topography in the Aleutian Islands is of two types: (a) wave-cut platforms less than 600 feet above sea level, bordered by low sea cliffs, and (b) intensely glaciated mountainous islands 600-3,000 feet above sea level, indented with fiords and bordered by cliffs as high as 2,000 feet.... Broad level intertidal platforms border some islands; they were probably produced by frost weathering."

The Commander Islands are the westernmost emergent parts of the Aleutian Ridge. They include two large islands, Bering and Copper. The Commander Islands are 156 km (97 mi) from Kamchatka and 290 km (180 mi) from Attu Island, the westernmost of the Aleutian Islands.

The Pribilof Islands are volcanic extrusions from the continental shelf of the Bering Sea (Wahrhaftig 1965). They include two large islands, St. Paul and St. George, two small islands, Otter and Walrus, and an islet, Sea Lion Rock. These islands are mainly of undissected topography, consisting of Cenozoic basalt flows and pyroclastic debris interbedded with some sediments. Cinder cones are present.

In most aspects, the rocky shores and islets occupied by harbor seals in the Commander, Aleutian, and Pribilof Islands are similar. Cobble and pebble beaches are present in protected bays and fjords, and sandy beaches occur at the mouths of a few of the short, swift streams. Muddy shores are nearly absent in these islands.

MATERIALS AND METHODS

Most of the materials utilized in this study were obtained by the authors in the course of four expeditions: Cruises of the RV *Alpha Helix* in Aleutian and Pribilof waters during 1968 (Burns), 1972 (Burns), and 1973 (Burns and Gol'tsev), and of the hunting vessel *Sanzar* in Commander Island waters in 1974 (Gol'tsev). Specimens were collected by shooting with a high-powered rifle. Some additional materials, mainly from the western Aleutian and Pribilof Islands, were made available by biologists of the Alaska Department of Fish and Game and the University of Alaska.

Seals collected by the authors were sexed, weighed, measured, photographed (skins wet), and necropsied. Measurements included standard length and axillary girth. Weights were of whole seals (with no correction for blood loss) and of the hide and attached blubber. For studies of growth, data from males and females were treated separately because of sexual dimorphism in size. Skulls were prepared for taxonomic studies reported elsewhere (Burns et al. 1984). Lower canine teeth were extracted, decalcified, and sectioned longitudinally to determine age, based on the number of annuli in the cementum (Bigg 1969a).

[6]Chapskii, K. K. 1975. Taxonomy of seals of the genus *Phoca sensu stricto*. *In* Marine mammals. Materials 6th all-union conf. 2:159-162. [Abstr.] Naukova Dumka, Kiev.

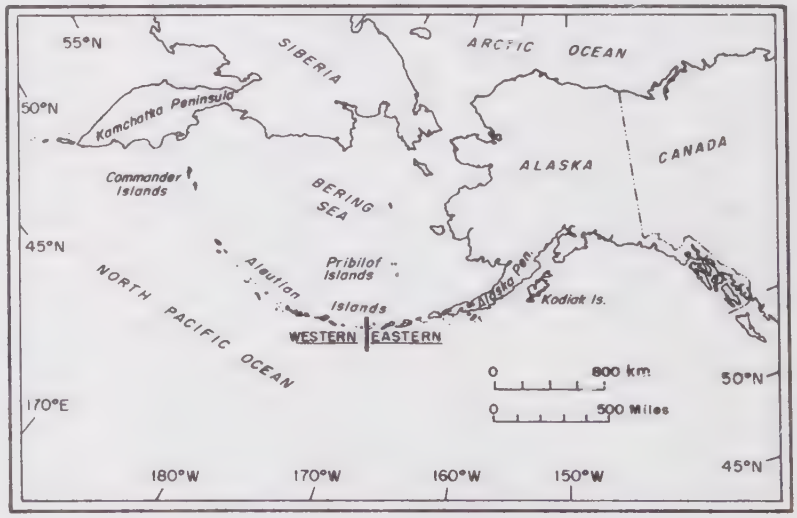


Figure 1.—Map of the North Pacific region showing the location of the study area.

Reproductive tracts were obtained from most females collected in Alaskan waters. These were preserved in 10% Formalin[7] for later study, at which time the uterine horns were externally examined for signs of current or previous pregnancy, indicated by external size, form, and degree of rugosity. Uterine horns were opened and examined for placental scars, fetuses, or other indications of recent pregnancy, including condition of the uterine walls, presence of hemorrhagic tissue, and kind and amount of debris in the lumen. Ovaries were serially sectioned longitudinally with a scalpel, in sections 1-2 mm thick. Each section was examined macroscopically for vesicular follicles, corpora lutea, and corpora albicantia. On the basis of the findings, females were classified as nulliparous, primaparous, or multiparous.

Our sample included 173 seals and 15 fetuses. Fifty-one of the seals were from the Commander Islands, 74 were from the Rat and Andreanof Islands of the central and western Aleutians, 35 were from the Islands of Four Mountains and Fox Islands of the eastern Aleutians, and 13 were from the Pribilof Islands (Fig. 1). For various reasons, we were unable to obtain all of the data desired from each seal; sample sizes for each data set are indicated where appropriate.

RESULTS

Habitat

Harbor seals were present in the nearshore waters of all parts of the study area. Their abundance tended to be greatest in protected inlets, bays, and fjords of the larger islands and least along simple, exposed coasts and around the smaller islands. One exception was Otter Island in the Pribilofs, where harbor seals were abundant around its exposed coast.

In the protected bays and fjords of the Aleutian Islands, seals usually were found in small groups on narrow boulder beaches or on nearshore rocky islets. In less protected areas they tended to haul out on the wider, more gently sloping beaches composed of small stones or gravel. The general size of groups on those beaches was much larger than that of groups on boulder beaches and islets. Where broad, gently sloping beaches occurred adjacent to rocky islets and boulder beaches, the seals hauled out mostly on the broad beaches. Sandy beaches also were utilized but are not common in the study area.

Abundance and Composition

Seals were least numerous around the Islands of Four Mountains, in the eastern Aleutians. During a census via small boat on 7 August 1973, we saw only seven seals along 7.2 km (4.5 mi) of the north side of Yunaska and 57 seals along approximately 22.5 km (14 mi) of Chuginadak. Although these densities are high in comparison to those in many other parts of the range of harbor seals, they were the lowest encountered by us in the Aleutian Islands. There were no protected embayments on those two islands.

Because the beaches utilized by seals in the study area usually were of black or dark volcanic rock, and because the seals also were mostly of dark coloration, assessment of their abundance required very close inspection. On several occasions when no seals or very few were seen from the ship anchored 1 to 2 km offshore, we found them actually to be numerous on closer inspection, when we walked the beaches or traveled very close to them in small boats.

Nearly two-thirds of the animals older than pups that we collected were females (48:82). In instances where several adult seals were taken from a group on shore, the animals commonly were all of one sex. Males predominated (7:1) in the seals taken in the water adjacent to large hauled out groups during July-August 1973.

Pelage

Shaughnessy and Fay (1977) summarized the data available on frequency of occurrence of light and dark color phases in harbor seals of the North Pacific region, including the four areas considered here. In their samples, dark phase seals occurred with a frequency of about 90% on the Commander Islands ($N=1,500+$), 80% on the western Aleutian Islands ($N=37$), 30% on the eastern Aleutian Islands ($N=348$), and 30% on the Pribilof Islands ($N=1,643$).

Most of our regional samples were smaller, being the number of animals actually collected. In these samples, the percentage frequency of dark phase seals was: Commander Islands, 59% ($N=51$); western Aleutians, 70% ($N=43$); eastern Aleutians, 50% ($N=10$); and Pribilof Islands, 40% ($N=5$). The proportion of dark seals on the Aleutian Islands was not significantly different from the proportion on the Commander Islands ($\chi^2=0.58$, $P > 0.25$). However, dark phase seals tended to occur more frequently in localities on the western part of the Aleutian Ridge than on the eastern part and the Pribilof Islands. This gradient continues to the west, with the highest proportion of dark phase seals on Hokkaido Island (Naito 1973; Shaughnessy and Fay 1977).

Age and Growth

The length/age and weight/age relationships for harbor seals collected in this study are presented in Tables 1 and 2. The probability of differences in size among the four samples was tested by the Kruskal-Wallis test (analysis of variance by ranks: Zar 1974), the results of which are shown in Table 3. In all cases, the null hypothesis was not rejected. This test was not applied to pups, because the times of sampling in each area were different, and growth in pups is rapid.

Since no differences in size were demonstrated among areas, data from seals in all areas were pooled. These suggest that about 70% of growth is achieved by age 6 or 7 (Figs. 2, 3). Length/age correlation is a better indicator of growth than weight/age in these seals, since there are large seasonal variations in weight, associated with pregnancy, lactation, and molt.

The average standard length of adult males 11 yr and older was 176.25 cm. The largest male, 191.0 cm (age and weight unknown), was from Amchitka Island. The heaviest male, 140.5 kg, was 14 yr old and was collected at Atka Island. The average standard length of adult females 11 yr and older was 161.82 cm; the maximum was 175.8 cm in a 25-yr-old female taken near Adak Island. This animal was lactating and had recently ovulated, as indicated by the presence of a developing corpus luteum; she weighed 122.4 kg. The heaviest female, 125.5 kg, was collected near Amchitka Island. She was 19 yr old and was carrying a near-term fetus weighing 13.6 kg. Comparison with sizes of adult seals from other areas around the North Pacific (Fig. 4) indicates that the Commander-Aleutian-Pribilof seals are not unusual.

Laws (1956) indicated that, in pinnipeds, the average length of females at puberty is about 86% of adult length. In our sample, females reached the 86% level at age 4. This corresponds well with

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1.—Standard length/age relationship for harbor seals, *Phoca vitulina*, from the Commander, western Aleutian, eastern Aleutian, and Pribilof Islands.

		Commander Is.			W. Aleutian Is.			E. Aleutian Is.			Pribilof Is.		
		SL (cm)			SL (cm)			SL (cm)			SL (cm)		
Sex	Age (yr)	*N*	Mean	Range	*N*	Mean	Range	*N*	Mean	Range	*N*	Mean	Range
Male	Pup	4	106.7	100.0-112.0	5	105.6	96.8-115.0	2	109.8	109.2-110.5	0	—	—
	1	0	—	—	1	—	112.0	1	—	125.0	0	—	—
	2	2	124.5	121.0-128.0	0	—	—	2	131.7	126.6-136.8	0	—	—
	3	1	—	130.0	0	—	—	3	145.9	140.3-154.9	0	—	—
	4	0	—	—	0	—	—	0	—	—	0	—	—
	5	1	—	147.0	0	—	—	1	—	147.3	0	—	—
	6	2	170.0	167.0-173.0	1	—	158.0	0	—	—	0	—	—
	7	4	158.7	156.0-163.0	2	162.0	162.0	1	—	157.5	0	—	—
	8	0	—	—	3	171.7	166.0-180.3	2	162.6	153.7-171.5	1	—	166.0
	9	1	—	174.0	0	—	—	2	166.6	161.3-172.0	0	—	—
	10	1	—	160.0	2	167.6	166.3-169.0	1	—	160.7	0	—	—
	11+	3	176.0	168.0-184.0	7	180.4	166.0-191.0	3	166.8	159.1-171.4	0	—	—
Female	Pup	4	107.0	100.0-114.0	9	103.1	87.6-119.0	4	112.3	104.5-119.0	1	—	123.1
	1	2	118.5	117.0-120.0	3	118.8	116.2-122.2	2	117.2	113.7-120.7	0	—	—
	2	1	—	128.0	1	—	127.6	1	—	127.0	1	—	123.8
	3	5	126.8	119.0-131.0	3	139.9	135.2-143.0	0	—	—	0	—	—
	4	4	132.7	127.0-137.0	3	143.3	138.0-146.0	2	145.7	135.2-156.2	0	—	—
	5	4	146.2	140.0-155.0	5	139.8	121.0-152.4	1	—	144.8	0	—	—
	6	3	151.0	144.0-155.0	5	149.3	132.0-162.5	1	—	146.0	1	—	148.5
	7	4	144.7	142.0-147.0	1	—	141.7	4	148.0	140.0-160.0	0	—	—
	8	3	151.0	146.0-157.0	2	158.4	154.9-161.9	0	—	—	1	—	155.5
	9	0	—	—	1	—	153.0	1	—	137.5	0	—	—
	10	0	—	—	1	—	150.4	0	—	—	0	—	—
	11+	2	165.0	158.0-172.0	16	161.5	148.1-175.8	0	—	—	[1]1	—	160.5

[1]From Scheffer (1977).

Table 2.—Weight/age relationship for harbor seals, *Phoca vitulina*, from the Commander, western Aleutian, eastern Aleutian, and Pribilof Islands.

		Commander Is.			W. Aleutian Is.			E. Aleutian Is.			Pribilof Is.		
		Weight (kg)			Weight (kg)			Weight (kg)			Weight (kg)		
Sex	Age (yr)	*N*	Mean	Range	*N*	Mean	Range	*N*	Mean	Range	*N*	Mean	Range
Male	Pup	4	29.7	26.0-31.0	5	29.2	24.1-34.0	2	30.1	26.8-33.5	0	—	—
	1	0	—	—	2	43.3	38.6-48.0	1	—	44.4	0	—	—
	2	2	51.5	48.0-55.0	0	—	—	2	54.0	52.6-55.5	0	—	—
	3	1	—	59.0	0	—	—	3	59.3	55.5-66.2	0	—	—
	4	0	—	—	0	—	—	0	—	—	0	—	—
	5	1	—	72.0	0	—	—	1	—	68.2	0	—	—
	6	2	101.0	96.0-106.0	1	—	88.6	0	—	—	0	—	—
	7	4	93.5	78.0-120.0	2	82.9	77.3-88.6	1	—	87.3	0	—	—
	8	0	—	—	2	105.4	95.2-115.6	2	91.1	75.0-107.3	1	—	88.4
	9	1	—	103.0	0	—	—	2	105.5	100.0-111.1	0	—	—
	10	1	—	104.0	2	117.6	117.3-117.9	1	—	84.1	0	—	—
	11+	3	113.0	92.0-125.0	5	125.4	107.7-140.5	3	100.5	87.0-123.6	0	—	—
Female	Pup	4	28.5	24.0-32.0	10	29.1	15.9-38.5	5	31.4	24.1-39.9	1	—	35.3
	1	2	38.5	33.0-40.0	2	36.2	34.5-38.0	2	37.0	30.5-43.6	0	—	—
	2	1	—	53.0	1	—	40.8	1	—	45.3	1	—	38.5
	3	5	45.6	33.0-54.0	3	54.7	47.6-62.7	0	—	—	0	—	—
	4	4	50.0	41.0-60.0	1	—	68.0	2	59.6	53.5-65.7	0	—	—
	5	4	63.7	54.0-78.0	3	65.8	47.6-81.6	1	—	76.4	0	—	—
	6	3	73.3	72.0-76.0	4	71.1	50.7-84.3	1	—	54.5	1	—	63.4
	7	4	74.2	65.0-86.0	1	—	63.4	4	70.0	60.0-86.8	0	—	—
	8	3	75.3	64.0-84.0	2	71.1	63.4-78.9	0	—	—	1	—	79.3
	9	0	—	—	0	—	—	1	—	54.0	0	—	—
	10	0	—	—	1	—	68.0	0	—	—	0	—	—
	11+	2	91.0	78.0-104.0	16	94.4	56.2-125.5	0	—	—	[1]1	—	106.2

[1]From Scheffer (1977).

Table 3.—Results of Kruskal-Wallis analysis of variance by ranks, as applied to length/age correlations per sex from the four sample areas: 1 = Commander Islands, 2 = western Aleutians, 3 = eastern Aleutians, and 4 = Pribilof Islands. The hypothesis tested is that the groups compared are similar (null hypothesis).

Areas compared	Age class (yr)	Sex	Calculated H value	Critical table value[1] ($P = 0.01$)	Null hypothesis
1 × 2 × 3	1	F	0.18	9.21	accepted
1 × 2 × 3	4	F	4.00	6.44	accepted
1 × 2 × 3 × 4	6	F	0.36	11.34	accepted
1 × 2 × 4	11+	F	7.28	9.21	accepted
2 × 3 × 4	8	M	0.81	9.21	accepted
1 × 2 × 3 × 4	11+	M	2.43	11.34	accepted

[1]Critical values are from tables of Critical Values of the Kruskal-Wallis H, or Critical Values of the Chi-Square Distribution, as appropriate, depending upon sample size (Zar 1974).

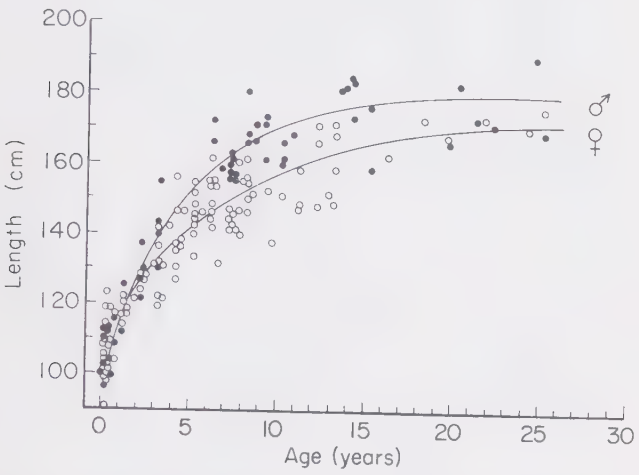


Figure 2.—Standard length per age of harbor seals, *Phoca vitulina*, from the Commander, Aleutian, and Pribilof Islands. Curve was fitted visually.

our findings from the reproductive organs, as described below. The standard length (SL) of pups taken in late July and early August was 61% (males) and 66% (females) of the mean adult length (11 yr and older).

Axillary girths (sexes combined) were 66.9% SL in pups (range 58.6-75.8%, $N=21$) and 64.3% SL in animals 11 yr and older (range 56.1-78.9%, $N=28$). The seasonal samples are small but show trends in variation similar to those of percentage weight of skin and blubber (Table 4).

The percentage of total body weight made up by skin and blubber varied seasonally among age classes (Table 4). In July and August, pups (near and recent weanlings) had the highest mean percentage

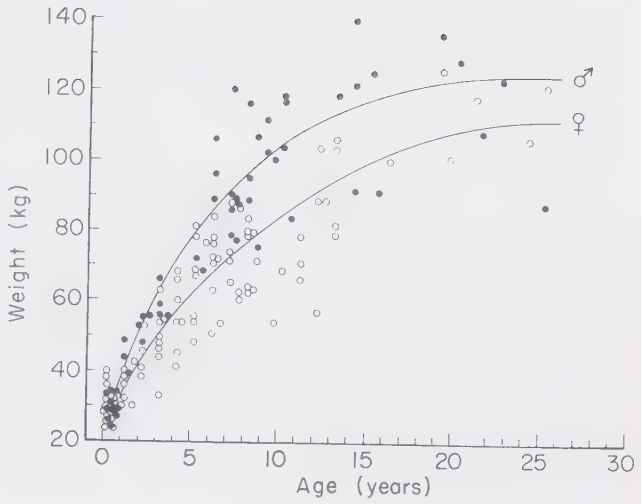


Figure 3.—Body weight per age of harbor seals, *Phoca vitulina*, from the Commander, Aleutian, and Pribilof Islands. Curve was fitted visually.

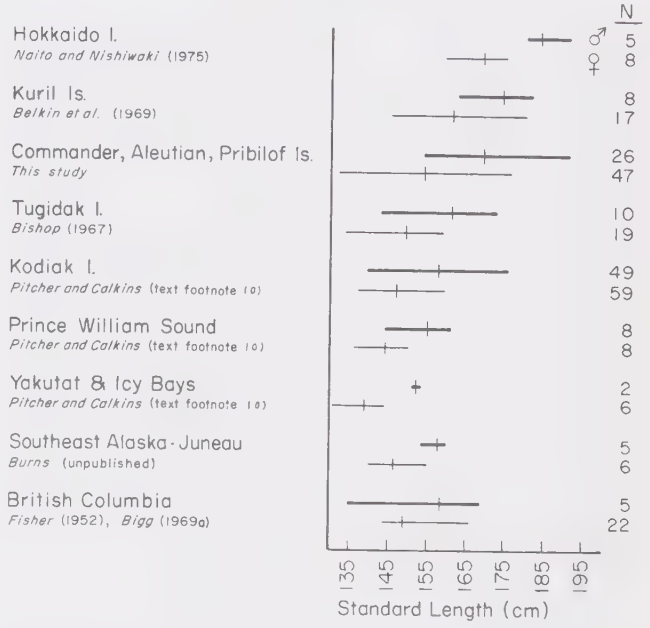


Figure 4.—Maximum, minimum, and mean standard lengths of harbor seals, *Phoca vitulina*, from the North Pacific region. Males were 8 yr and older, females 6 yr and older. Values were derived from the best approximations of growth curves, tables, or texts of the indicated sources.

Table 4.—Percent of total body weight made up of skin and blubber, and axillary girth/standard length × 100 (coefficient of condition) in harbor seals, *Phoca vitulina*, from Aleutian, Commander, and Pribilof Islands.

Area	Collection period	Age group	Skin and blubber as % body weight			AG/SL × 100 (coeff. cond.)		
			N	Mean	Range	*N*	Mean	Range
Aleutian Is.	22 July-11 Aug.	pup	11	47.1	36.3-55.8	6	71.2	67.5-75.8
		1 yr	3	40.7	36.7-45.5	3	66.4	64.4-67.8
		≥ 2	33	34.9	22.9-53.4	35	63.3	56.1-73.2
	Nov.-Apr.	pup	3	33.0	25.9-37.3	7	64.3	58.6-71.0
		1 yr	1	37.4	—	2	66.9	63.6-70.3
		≥ 2	11	41.1	32.8-59.1	28	63.7	56.6-69.9
Commander Is.	15-30 Aug.	pup	8	40.6	31.2-52.9	8	66.1	62.1-72.0
		1 yr	2	35.1	30.3-40.0	2	65.0	64.2-65.8
		≥ 2	41	32.8	24.0-38.2	41	64.2	55.5-74.1
Pribilof Is.	12 Aug.	≥ 2	4	30.9	27.7-35.5	4	63.4	61.2-65.6

of hide and blubber. Seals 2 yr old and older had the lowest values; those 1 yr old were intermediate. This trend was the same in the Aleutian, Commander, and Pribilof Islands. In November to April the ranking was reversed.

Reproduction

Reproductive tracts were obtained from 76 females taken in the Aleutian and Pribilof Islands. Of these, 15 were from pups, 13 were from animals between ages 1 and 5 that had not yet ovulated, and 48 were from females between ages 3 and 25 that had ovulated at least once.

In the second half of July, only 4 (29%) of 14 sexually mature females had ovulated, but by the first half of August, 10 (77%) of 13 had ovulated (Table 5). These findings indicate that the breeding (mating) period of harbor seals in the Aleutian-Pribilof area extends from at least mid-July to mid-August, probably with a peak in early August.

Table 5.—Condition of ovarian structures in 27 sexually mature female harbor seals, ages 4 and older, taken between 12 July and 12 August on the Aleutian and Pribilof Islands.

		Enlarged follicles only		Recent ovulation		Corpus luteum partly formed		Corpus luteum completely formed	
Time period	*N*	No.	%	No.	%	No.	%	No.	%
12-31 July	14	10	71.4	2	14.3	1	7.1	1	7.1
1-12 August	13	3	23.1	3	23.1	3	23.1	4	30.7

Three females taken in October had a large corpus luteum but no implanted fetus. Two taken on 6 November exhibited slight enlargement of implantation sites, indicating that implantation had just taken place. In each of these, the embryo was < 1 mm long. One female taken on 8 December contained an 11.4 g fetus, 8.2 cm in crown-rump length. These data indicate that implantation takes place early in November, about 3 mo after mating. Lengths and weights of 16 fetuses and one newborn pup from the Aleutian and Pribilof Islands are presented in Table 6.

Time of birth was determined on the basis of the latest occurrence of near-term fetuses and the earliest occurrence of recently postpartum females. The latter were identified from the condition of the uterus, in which one horn still was distended and in some cases filled with blood and debris from a very recent birth. Each of two females, taken on 2 June at Amchitka Island, supported a near-term fetus, 13.6 and 11.8 kg. One taken on 5 July appeared to have given birth very recently. Each of nine females taken between 24 and 31 July showed signs of recent birth; at least four of these probably had given birth within the previous 2 wk.

Thus, the birth period in the Aleutian area seems to extend at least from mid- or late June to mid-July, with the majority of births presumed to occur in late June to early July. Murie (1959) reported newborn pups in the Aleutians in mid-June. On the Commander Islands, births occur to the end of June (Marakov 1967). Johnson (1974)[8] found births taking place on the Pribilof Islands in June and July with the greatest number in late June-early July. Scheffer (1977) indicated mid-May to mid-July as the birth period on the Pribilofs, but some of the pups reported by him could have been *P. largha*.

[8]Johnson, B. W. 1974. Otter Island harbor seals: a preliminary report. Unpubl. manuscr., 20 p. Alaska Dep. Fish Game, Fairbanks, AK 99701.

Table 6.—Standard length and weight of fetal and newborn harbor seals, *Phoca vitulina*, from the Aleutian and Pribilof Islands, Alaska.

Date	Location	Sex	Weight (g)	Standard length (cm)
6 Nov.	Amchitka	?[1]	1	1
6 Nov.	Amchitka	?[1]	1	1
8 Dec.	Amchitka	M	11.4	8.2
28 Jan.	Amchitka	F	614.0	27.0
4 Mar.	Unalaska	F	2,526.5	48.3
15 Mar.	Adak	F	3,292.0	55.0
10 Apr.	Unalaska	F	5,421.5	65.1
13 Apr.	Unalaska	F	5,875.5	68.6
13 Apr.	Otter	M	5,023.0	66.9
13 Apr.	Otter	M	6,560.0	72.4
13 Apr.	Otter	M	5,763.0	68.3
4 May	Tanaga	?	9,070.0	—
6 May	Tanaga	?	8,620.0	—
2 June	Amchitka	F	13,620.0	88.0
2 June	Amchitka	F	11,804.0	76.0
10 June	Otter	M[2]	11,100.0	89.8 (newborn)
15 June	St. Paul	F[2]	13,800.0	91.5

[1]Specimens provided by R. L. Rausch.
[2]From Scheffer (1977).

Of 16 sexually mature females collected during November to early June, 12 (75%) were supporting an apparently healthy fetus. Of the remainder, one taken in March showed no indications of recent pregnancy; another in March contained a partly resorbed fetus; and two taken in April had recently aborted. Of 12 adult seals taken in July, 9 (75%) had recently given birth; the others showed no indication of recent pregnancy.

Age at first ovulation was from 3 to 5 yr (Table 7). All females 6 yr old and older had ovulated at least once. The youngest seals in our sample which were successful in pregnancy were 5 yr old. One of these contained a near-term fetus on 10 April; the other had given birth not long before it was collected (24 July). The latter also had been pregnant in the previous year, judging from the presence of a placental scar in the opposite uterine horn and presence of a large corpus albicans in the adjacent ovary.

Table 7.—Incidence of ovulation in 21 harbor seals, ages 2 to 7 yr, taken on the Aleutian and Pribilof Islands during July-August.[1]

Age	*N*	Ovulated %
2	3	0
3	3	33
4	5	60
5	3	67
6	5	100
7	2	100

[1]An animal was considered to have ovulated if a corpus luteum, a corpus albicans, or a follicle larger than 13 mm was present.

Feeding Habits

Remains of food were found in 16 of 51 seals taken on the Commander Islands between 15 and 30 August. Fourteen of these contained only beaks of octopus, one contained octopus and uniden-

tified fishes, and one contained squid beaks. Similar prey were reported for harbor seals about the Kuril Islands (Panina 1966). Since cephalopod beaks may accumulate from several feedings, their presence is not representative of the proportion of cephalopods in the diet (Pitcher 1980). Fishes, cephalopods, and shrimps were indicated by Marakov (1967) as the prinicpal foods of harbor seals near the Commander Islands.

Food remains were found in 17 of 43 seals taken in the western Aleutian Islands between 25 July and 6 August. Four of these were nursing pups, the stomachs of which contained only milk. Most of the remaining 13 seals had fed on only one type of prey. Three stomachs from weaned pups and two from older animals contained mysids; four contained pandalid shrimps; three contained remains of octopus; and one contained a combination of crangonid shrimps and fishes (Pacific cod, *Gadus macrocephalus*, and unidentified sculpin). The prey of 18 harbor seals from Amchitka Island, as reported by Wilke (1957) and Kenyon (1965), included mainly octopus; Atka mackeral, *Pleurogrammus monopterygius*; and greenling, *Hexagrammos* sp.

Our findings in the pups indicate that the time of weaning is in late July to early August, and suggest that the pups' first solid food in this area may be mysids. These organisms were very abundant in dense swarms within the kelp beds, where they probably are readily available to the pups.

The stomachs of three seals from the eastern Aleutians contained food. These were collected at Unalaska Island, between 10 and 13 April. Walleye pollock, *Theragra chalcogramma*, was the dominant prey, comprising 98% of the total volume. Pacific cod comprised the remaining 2% (Lowry et al. 1979).

Stomachs of eight seals from the Pribilof Islands contained food. These were obtained in mid-April. Data from these seals were pooled and treated as a single sample. The mean volume of stomach contents per seal was 166.2 ml. Fishes, principally walleye pollock and cods (*Gadus* spp.), comprised 63.5% of the total volume. Octopus made up 28.7% of the volume.[9]

DISCUSSION AND CONCLUSIONS

The differences among harbor seals from the Asian coast, the Aleutian-Commander Ridge, and the North American coast are not inconsistent with predictions for a relatively sedentary species exhibiting essentially linear distribution over an elongate, coastal range. Based on the values reported by other investigators (see Fig. 4), growth of harbor seals from the Asian and North American coasts appears to be comparable with that of seals from the Commander-Aleutian area. The Asian and Commander-Aleutian seals tend to be larger and more often of dark pelage than those from most of North America. North American seals tend to be smallest and palest in the northern part of the Gulf of Alaska and in northern British Columbia (Fig. 4 and see Shaughnessy and Fay 1977). Perhaps the larger size of seals occupying the Aleutian-Commander and Kuril-Kamchatka Ridges may be a phenotypic expression of the richness of their environment, which includes some of the most productive marine habitats in the world.

A study of the genetics of North Pacific harbor seals has suggested that the basic dark and light color phases are controlled by a single pair of autosomal alleles, with light phase dominant, and no correlation with sex or size within local populations (Kelly 1981). Investigation of cranial characteristics has indicated that differences between groups in skull size parallel those of body length, and that proportional relationships of skull measurements among groups are similar (Burns et al. 1984).

From Hokkaido to the eastern Aleutians, differences between regional groups in the timing of events in the breeding cycle are small and apparently clinal (Bigg 1969b, 1973). In eastern Hokkaido, implantation of the fetus takes place appreciably earlier than was found in our study. Naito and Nishiwaki (1972) reported fetuses 3.9, 8.4, 8.5, and 9.5 cm long in females collected during October from the Nemuro Peninsula, whereas our findings suggest attainment of such size no earlier than November. They indicated further that birth takes place in May and June, and that weaning is completed by late June-early July (Naito and Nishiwaki 1972, 1973), both about 1 mo earlier than in our study area. Time of birth on the Kuril Islands apparently is similar to that on Hokkaido (Belkin 1964; Belkin et al. 1969; Velizhanin 1967). On islands in the Gulf of Alaska also, implantation and birth take place somewhat earlier than on the Aleutian Islands. Bishop (1967) and Pitcher and Calkins (1979)[10] observed that implantation takes place in late August to early October and birth primarily in May and June, at least 2 wk earlier than in our study area. Shaughnessy and Fay (1977) summarized the available information from other areas farther south on the North American coast and suggested, as did Bigg (1973), that the observed variation in birth dates may be correlated with local availability of certain prey during the period when pups are weaned.

The Commander-Aleutian Ridge is of particular zoogeographic importance to marine mammals because it extends across the entire northern end of the North Pacific Ocean and supports continuous North American-Asian distributions of such species as the sedentary sea otter, *Enhydra lutris*, the more wide-ranging Steller sea lion, *Eumetopias jubatus*, and harbor seals. For the seals, the habitats utilized, size/age relationships, timing of events in the annual breeding cycle, and feeding habits appear to be essentially the same throughout this area as well as on the Pribilof Islands. Only pelage coloration appears to vary, but in an east-west clinal manner. Thus, to the extent that our investigations compared them, we found no significant biological or ecological differences among the seals of the Aleutian-Commander region. Instead, our results indicate a single, linearly distributed form of harbor seals in this region, as predicted by Mohr (1965), Chapskii (1969), Bychkov (1971), Burns and Fay (footnote 5), Kosygin et al. (footnote 3), Shaughnessy and Fay (1977), and Burns et al. (1984).

Harbor seals in the Aleutian and Pribilof Islands are unexploited and, for the most part, undisturbed. Their populations probably exist in balance with the natural carrying capacity of their environment. For this reason, we believe that the various biological characteristics described in this study are those of stationary populations, in which birth and death rates have been equal for a long time. These are of considerable significance for comparative purposes. For example, the pregnancy rate (75%) for sexually mature females in our study area is markedly lower than that of a heavily exploited and declining population (95%) in eastern Canada (Boulva and McLaren 1979) and of an exploited population (97%) in British Columbia (Bigg 1969a). Pitcher and Calkins (footnote 10) found a pregnancy rate of 92% for adults in the Gulf of Alaska, where the population is presumed to be increasing following earlier intensive harvests.

[9]L. F. Lowry, Game Biologist II, Alaska Dep. Fish Game, Fairbanks, AK 99701, pers. commun. October 1979.

[10]Pitcher, K. W., and D. G. Calkins. 1979. Biology of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Final Report, R.U. 229, 72 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

ACKNOWLEDGMENTS

We wish to express our appreciation to J. Vania, K. B. Schneider, K. W. Pitcher, K. J. Frost, L. F. Lowry, L. M. Shults, and R. L. Rausch for making specimens available to us. L. F. Lowry examined the food remains in seals from the Aleutian and Pribilof Islands. K. W. Pitcher provided unpublished data about harbor seals in south-central Alaska. F. H. Fay was especially helpful, providing enlightening discussions and critical reviews of this paper. M. Bigg, K. W. Pitcher, and J. Coady also kindly reviewed the manuscript, D. Borchert prepared the figures, and K. Valentine typed the several drafts. The research vessels MV *Alpha Helix*, operated by the Scripps Institution of Oceanography, USA, and the KS *Sanzar*, operated by the Pacific Research Institute of Fisheries and Oceanography (TINRO), USSR, provided the principal logistic support. We are indebted to the officers and crews of these vessels. R. Elsner, Chief Scientist during the 1973 cruise of the *Alpha Helix*, was particularly accommodating and helpful. Financial support was provided by TINRO (Gol'tsev) and by Federal Aid in Wildlife Restoration, Projects W-17-R, and the Alaska Sea Grant Program (Burns).

LITERATURE CITED

BELKIN, A. N.
1964. A new species of seal from the Kuril Islands—*Phoca insularis* sp. n. Dokl. Akad. Nauk SSSR 158:1217-1220.

BELKIN, A. N., G. M. KOSYGIN, and K. I. PANIN.
1969. New data on the characteristics of the insular seal. *In* V. A. Arsen'ev, B. A. Zenkovich, and K. K. Chapskii (editors), Marine mammals, p. 157-175. Nauka, Moscow.

BIGG, M. A.
1969a. The harbour seal in British Columbia. Fish. Res. Board Can., Bull. 172, 33 p.
1969b. Clines in the pupping season of the harbour seal, *Phoca vitulina*. J. Fish. Res. Board Can. 26:449-455.
1973. Adaptations in the breeding of the harbour seal (*Phoca vitulina*). J. Reprod. Fert., Suppl. 19:131-142.

BISHOP, R. H.
1967. Reproduction, age determination, and behavior of the harbor seal, *Phoca vitulina* L., in the Gulf of Alaska. M.S. Thesis, Univ. Alaska, Fairbanks, 121 p.

BOULVA, J., and I. A. McLAREN.
1979. Biology of the harbor seal, *Phoca vitulina*, in eastern Canada. Fish. Res. Board Can., Bull. 200, 24 p.

BURNS, J. J.
1970. Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi Seas. J. Mammal. 51:445-454.

BURNS, J. J., and F. H. FAY.
1973. Comparative biology of Bering Sea harbor seal populations. [Abstr.] Proc. Alaska Sci. Conf. 23:48.

BURNS, J. J., F. H. FAY, and G. A. FEDOSEEV.
1984. Craniological analysis of harbor and spotted seals of the North Pacific region. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:5-16.

BYCHKOV, V. A.
1971. Review of the status of pinnipeds of the fauna of the USSR. *In* L. K. Shaposhnikov, V. A. Borisov, L. V. Zhirnov, and N. V. Shkarban (editors), Scientific elements of nature conservation, p. 59-74. Ministerstvo Sel'skogo Khozyaistva, Moscow.

CHAPSKII, K. K.
1960. Morphologie systematique, differenciation intra-specifique et phylogenese du sous-genre *Phoca sensu stricto*. Mammalia 24:343-360.
1967. Morpho-taxonomic characteristics of the pagetoda form of the Bering Sea larga. *In* K. K. Chapskii and M. Y. Yakovenko (editors), Investigations of marine mammals, p. 147-176. Polyarnaya Pravda, Murmansk.
1969. Taxonomy of seals of the genus *Phoca sensu stricto* in the light of contemporary craniological data. *In* V. A. Arsen'ev, B. A. Zenkovich, and K. K. Chapskii (editors), Marine mammals, p. 294-304. Nauka, Moscow.

FISHER, H. D.
1952. The status of the harbour seal in British Columbia, with particular reference to the Skeena River. Fish. Res. Board Can. Bull. 93, 58 p.

HEPTNER, V. G., K. K. CHAPSKII, V. A. ARSEN'EV, and V. E. SOKOLOV (editors).
1976. Mammals of the Soviet Union. Vol. 2, pt. 3. Pinnipeds and toothed whales. Vysshaya Shkola, Moscow, 718 p.

INUKAI, T.
1942. Hair seals from the northern waters of Japan. [In Jpn.] Shokubutsu Oyobi Dobutsu 10:927-932, 1025-1030. (Engl. transl., Marine Mammal Div., Northwest Fish. Cent., Seattle, Wash.)

KELLY, B. P.
1981. Pelage polymorphism in Pacific harbor seals. Can. J. Zool. 59:1212-1219.

KENYON, K. W.
1965. Food of harbor seals at Amchitka Island, Alaska. J. Mammal. 46:103-104.

LAWS, R. M.
1956. Growth and sexual maturity in aquatic mammals. Nature (Lond.) 178:193-194.

LOWRY, L. F., K. J. FROST, and J. J. BURNS.
1979. Potential resource competition in the southeastern Bering Sea: fisheries and phocid seals. Proc. Alaska Sci. Conf. 29:287-296.

MARAKOV, S. V.
1967. Materials on the ecology of the larga of the Commander Islands. *In* K. K. Chapskii and M. Y. Yakovenko (editors), Investigations of marine mammals, p. 126-136. Polyarnaya Pravda, Murmansk.

MOHR, E.
1965. Über *Phoca vitulina largha* Pallas, 1811 und weissgeborene Seehunde. Z. Saeugetierkd. 30:273-287.

MURIE, O. J.
1959. Fauna of the Aleutian Islands and Alaska Peninsula. North Am. Fauna 61, 406 p. U.S. Fish Wildl. Serv., Washington, D.C.

NAITO, Y.
1973. Comparison in colour pattern of two species of harbour seal in adjacent waters of Hokkaido. Sci. Rep. Whales Res. Inst. 25:301-310.
1974. The hyoid bones of two kinds of harbour seals in the adjacent waters of Hokkaido. Sci. Rep. Whales Res. Inst. Tokyo 26:313-320.
1976. The occurrence of the phocid seals along the coast of Japan and possible dispersal of pups. Sci. Rep. Whales Res. Inst. Tokyo 28:175-185.

NAITO, Y., and M. NISHIWAKI.
1972. The growth of two species of the harbour seal in the adjacent waters of Hokkaido. Sci. Rep. Whales Res. Inst. Tokyo 24:127-144.
1973. Kurile harbour seal (*Phoca kurilensis*). *In* Seals: Proceedings of a working meeting of seal specialists on threatened and depleted seals of the world, held under the auspices of the Survival Service Commission of IUCN. Int. Union Conserv. Nature Nat. Resour. Publ., n.s., Suppl. Pap. 39:44-49.
1975. Ecology and morphology of *Phoca vitulina largha* and *Phoca kurilensis* in the southern Sea of Okhotsk and north east of Hokkaido. *In* K. Ronald and A. W. Mansfield (editors), Biology of the seal, p. 379-386. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169.

PANINA, G. K.
1966. On the feeding of the sea lion and hair seals on the Kuril Islands. Izv. TINRO 58:235-236.

PITCHER, K. W.
1980. Stomach contents and feces as indicators of harbor seal, *Phoca vitulina*, foods in the Gulf of Alaska. Fish. Bull., U.S. 78:797-798.

SCHEFFER, V. B.
1977. Newborn harbor seals on the Pribilof Islands, Alaska. Murrelet 58:44.

SHAUGHNESSY, P. D., and F. H. FAY.
1977. A review of the taxonomy and nomenclature of north Pacific harbour seals. J. Zool. (Lond.) 182:385-419.

VELIZHANIN, A. G.
1967. A new species of seal. Priroda 1967(7):76-79.

VORONOV, B. G.
1974. Mammals of the Kuril Islands. Akad. Nauk SSSR, Leningrad, 162 p.

WAHRHAFTIG, C.
1965. Physiographic divisions of Alaska. U.S. Geol. Surv. Prof. Pap. 482, 52 p.

WILKE, F.
1957. Food of sea otters and harbor seals at Amchitka Island. J. Wildl. Manage. 21:241-242.

ZAR, J. H.
1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J., 620 p.

Habitat Partitioning by Ice-Associated Pinnipeds: Distribution and Density of Seals and Walruses in the Bering Sea, April 1976

HOWARD W. BRAHAM,[1] JOHN J. BURNS,[2] GENNADII A. FEDOSEEV,[3] and BRUCE D. KROGMAN[1]

ABSTRACT

Aerial surveys were conducted over the Bering Sea pack ice in April 1976 to assess the distribution and density of five ice-associated pinnipeds. Results from those surveys support the hypothesis that walruses, ringed, ribbon, spotted, and bearded seals partition the available ice habitat by distributing themselves differentially according to north-south and east-west gradients. Partitioning is believed to be the result of selection for specific ice types and, perhaps, availability of different prey. All species exhibited a clumped distribution. Walruses were most abundant near St. Lawrence Island and in outer Bristol Bay, as had been observed in previous surveys during April. Ringed seals were widely dispersed, and their presence in considerable numbers in the southeastern sector of the pack is reported for the first time. Ribbon seals were most abundant in the west-central ice front. Densities of spotted seals were highest in the ice front, east and west of the major concentration of ribbon seals as well as in outer Bristol Bay. Bearded seals were nearly ubiquitous on the pack ice but with higher densities in the northern than in the southern sectors. The pack ice in April 1976 extended nearly to its southern maximum, hence the data collected during this study allowed a comparison of the spatial relationship among the ice-associated pinnipeds in a year of maximal dispersal.

РЕЗЮМЕ

В апреле 1976 г. были проведены аэровизуальные наблюдения за распределением и плотностью залегания пяти видов ластоногих на льдах Берингова моря. Результаты этих наблюдений подкрепляют гипотезу дифференцированного распределения моржа, акибы, крылатки, ларги, и лахтака соответственно с севера на юг и с востока на запад.

Предполагается, что такое распределение обусловлено выбором определенного типа льда, а также доступностью предпочитательной пищи.

Распределение всех видов имело пятнистый характер. Наибольшая численность моржей отмечалось близ острова Св. Лаврентия и по периферии зал. Бристоль, как, и в предыдущие годы. Кольчатая нерпа широко распространена и впервые в изобилии отмечалось в юго-восточной части ледового покрова. Наибольшее количество крылатки отмечено в западно-центральной части ледового фронта. Самая высокая плотность ларги была вдоль ледого фронта к востоку и западу от основных сосредоточений крылатки, а также в зал. Бристоль. Лахтак встречался почти повсеместно на паковом льду и плотность его скоплений была выше на севере, чем на юге.

Поскольку лёд в апреле 1976 г. простирался на юг до максимальных значений, полученные данные по распределению ластоногих характерны для года с максимальной ледовитостью моря.

INTRODUCTION

In winter and early spring, much of the Bering Sea is covered with ice floes, which are used as haul out areas by several species of pinnipeds: The Pacific walrus, *Odobenus rosmarus divergens*; the ringed seal, *Phoca hispida*; the ribbon seal, *Phoca fasciata*; the spotted or larga seal, *Phoca largha*; and the bearded seal, *Erignathus barbatus*. These pinnipeds use the ice as a substrate on which to give birth to their young, to molt, and to rest. To some extent also, the moving ice serves as a means for passive dispersal of these mammals into seasonal feeding areas, especially during its southward advance in autumn and its northward retreat in spring (Burns 1970; Fay 1974). Harbor seals, *Phoca vitulina*, and northern sea lions, *Eumetopias jubatus*, also rest on floes in the southern edge of the pack during the spring, particularly when it extends far into the southwestern and southeastern Bering Sea. The centers of abundance for those two pinnipeds, however, lie farther to the south, in ice-free areas such as the Aleutian and Commander Islands and the Alaska and Kamchatka Peninsulas. Their use of the pack ice, therefore, is irregular and opportunistic.

Pack ice generally is present over most of the continental shelf of the Bering Sea from December to June (Shapiro and Burns 1975; McNutt 1981). In most years, the pack reaches its maximum in extent during late March, when its extreme southern limit coincides approximately with the 200 m isobath (Burns and Harbo 1977[4]). In years of extreme icing, however, the maximum is attained in April

[1]National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115, USA.

[2]Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701, USA.

[3]Magadan Branch, Pacific Research Institute of Fisheries and Oceanography (MoTINRO), Nagaevskaya 51, Magadan 685013, USSR.

[4]Burns, J. J., and S. J. Harbo, Jr. 1977. An aerial census of spotted seal, *Phoca vitulina largha*, and walruses, *Odobenus rosmarus* in the ice front of Bering Sea. *In* Environmental assessment of the Alaskan continental shelf. Quarterly reports of principal investigators, April-June 1977, Vol. 1, p. 58-132. NOAA Environ. Res. Lab., Boulder, Colo.

and extends farther south. This was its condition in April 1976 (Fig. 1).

The spring distribution of pinnipeds in parts of the Bering Sea pack ice had been investigated previously, for example by Kenyon (1960[5], 1972[6]), Krylov et al. (1964), Tikhomirov (1964), Fedoseev (1965), Shustov (1965, 1969), Kosygin (1966), Burns (1970), and Fay (1974), but no single study had investigated distribution throughout the pack ice, as we were able to do in April 1976. April is the optimal month for such an investigation, for the greatest proportion of the species occurring there at that time is likely to be lying out on the ice, where they can be seen from the survey aircraft.

Three separate aerial surveys were conducted over the Bering Sea pack ice in April 1976, with the common objective of describing the distribution and density of the several species of pinnipeds residing there. Surveys were conducted over 1) the eastern Bering Sea by the National Marine Fisheries Service (H. W. Braham), 2) the ice front in the southeastern and southcentral Bering Sea by the Alaska Department of Fish and Game (J. J. Burns), and 3) the western Bering Sea by the Pacific Institute of Fisheries and Oceanography (G. A. Fedoseev). Although these surveys were conducted independently of each other, they were coordinated for purposes of obtaining maximal areal coverage and compatible data. Because the ice cover was more extensive than normal, we hypothesized that the distribution of the pinnipeds also would be near its maximum in extent. The aerial surveys conducted at that time offered an unusual opportunity to test that hypothesis. The purpose of this paper is to report on the combined results.

NATURAL HISTORY OF THE SPECIES SURVEYED

The distribution and movements of the ice-associated pinnipeds in the study area are closely linked with the advance and retreat of the pack ice (Burns 1970; Fay 1974). A major part of the Pacific walrus population migrates from the Bering Sea into the Chukchi Sea from April to June; they return to the Bering Sea in October to December (Belopol'skii 1939; Nikulin 1941; Fay 1982). In winter, the entire population is distributed throughout the Bering pack ice, but tends to concentrate in outer Bristol and Kuskokwim Bays and in the north-central Bering Sea near St. Lawrence Island (Kenyon footnotes 5, 6). Because they feed mainly on bivalve mollusks, walruses normally remain in waters <100 m deep, which coincides with the usual distribution of pack ice over the continental shelf. The young are born mainly in May, during the northward migration.

Ringed seals occur throughout the pack in the Bering Sea, with highest densities in areas of shore-fast ice (Fedoseev 1965; Johnson et al. 1966; Burns 1970, 1973[7]). This is the smallest of the ice-associated pinnipeds and it generally is solitary, congregating only during the molt in May-June. The subadults which have wintered in the Bering Sea begin to migrate northward in April; the adults and pups migrate later (Burns 1970, unpubl. data). During the winter, the highest concentrations of breeding adults occur 5-40 km offshore in the fast ice zone; juveniles and subadults tend to occur farther offshore (Tikhomirov 1966a; Burns 1970, footnote 7). The pups usually are born in the first week of April in snow lairs on fast ice, stable pack, or in pressure ridges (McLaren 1958; Burns 1970; Smith and Stirling 1975), hence the pups and attendant adults generally are not visible from the air during April.

Ribbon seals are unique to the North Pacific, occurring mainly in the Bering and Okhotsk Seas (Shustov 1965). Two "reproductive groups" in the Bering Sea were identified tentatively by Fedoseev and Shmakova (1976[8]), one in the western and the other in the eastern zone. Nevertheless, Fedoseev's (1984) craniological comparison suggests that considerable intermixing of these groups takes place. In April, ribbon seals characteristically occur on floes in the ice front, where they give birth to their pups from western Bristol Bay to within 50 km of the Soviet coast (Shustov 1965; Tikhomirov 1966a, b; Burns footnote 7; Fay 1974). Late spring concentrations have been reported in Anadyr Gulf and near St. Lawrence Island (Tikhomirov 1966a).

The spotted or larga seal, an ice-associated relative of the coastal harbor seal, frequents the ice front during winter and spring, with the greatest numbers within 25 km of the irregular southern edge of the pack. This seal is the most abundant species of the ice front in southeastern Bering Sea (Tikhomirov 1964). Although present throughout the front, the adults tend to congregate in eastern, central, and western zones. During April, the adults occur as isolated pairs, each with a single pup (Tikhomirov and Kosygin 1966; Burns et al. 1972); later, during the molt, they congregate in small herds and move northward to coastal and estuarine habitats in the northern Bering and Chukchi Seas.

Bearded seals are widely distributed throughout the Bering Sea pack ice in winter and spring, occurring principally in waters <200 m deep, wherever polynyas, leads, and thin ice persist (Burns 1970). In April, most bearded seals are solitary, except for females with pups; occasionally several seals may rest on the same floe. Highest densities in the pack ice have been reported near St. Lawrence Island, southeast of St. Matthew Island, south of Nunivak Island, and in Anadyr Gulf (Kosygin 1966). Local abundance may be related to availability of food (Tikhomirov 1964). The northward migration of bearded seals is underway in April (Burns 1967[9]); they later move northward into the Chukchi Sea with the retreating ice.

METHODS

Eastern Bering Sea Pack Ice Survey

The National Marine Fisheries Service (NMFS) survey covered the northeastern Bering Sea on 13, 15, 19-23 April and southeastern Bering and Bristol Bay on 6, 8, 9, 12, 13, 15, 17-19 April 1976 (Fig. 2). Strip census methods were applied, as described in Eberhardt (1978). Initially, the survey was stratified using randomly selected strips along lines of latitude 3 nmi (5.6 km) apart. Subsequently, strips were chosen systematically and the surveys flown to delineate further the areas of animal abundance (Krogman et al. 1978[10]). Stratification methods were used in the analysis to reduce the variance when estimating abundance.

[5]Kenyon, K. W. 1960. Aerial surveys of marine mammals in the Bering Sea, 23 February to 2 March 1960 and 25-28 April 1960. Unpubl. rep., 39 p. U.S. Bur. Sport Fish. Wildl., Seattle, WA 98115.

[6]Kenyon, K. W. 1972. Aerial surveys of marine mammals in the Bering Sea, 6-16 April 1972. Unpubl. rep., 79 p. U.S. Bur. Sport Fish. Wildl., Seattle, WA 98115.

[7]Burns, J. J. 1973. Marine mammal report. Project report, Fed. Aid Wildl. Restor., Vol. XIII, 44 p. Alaska Dep. Fish Game, Juneau, AK 99802.

[8]Fedoseev, G. A., and G. G. Shmakova. 1976. Some results of investigations of spatial structure of ribbon and larga seals of the Bering Sea. Unpubl. rep., 9 p. Special Meeting Marine Mammal Project, US-USSR Environmental Protection Agreement, Moscow.

[9]Burns, J. J. 1967. The Pacific bearded seal. Alaska Dep. Fish Game, Juneau, 66 p.

[10]Krogman, B. D., H. W. Braham, R. M. Sonntag, and R. G. Punsly. 1978. Early spring distribution, density, and abundance of the Pacific walrus (*Odobenus rosmarus*) in 1976. Final report, R.U. 14, 47 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

The survey aircraft were the turbo-jet powered Grumman Goose[11] (N780) and the long-range Lockheed Neptune P2V (N48347). The P2V was used only on 13 and 15 April. Airspeed generally was 120-140 kn at survey altitudes of 100-350 m; most surveys were flown at about 135 m. A crew of four people was used for most surveys; there were two observers, one recorder, and one alternate. Crew members changed jobs hourly to reduce observer fatigue. The alternate observer periodically surveyed from the rear of the aircraft to test for observer bias (e.g., for the number of animals missed by forward observers or to validate species identification).

Information recorded included species, number of adults and pups, local time of sighting, position to 1 nmi[2] (obtained from an onboard Global Navigation System, model GNS500), perpendicular angular distance from aircraft to animal (taken with an optical clinometer, model Pm-5/360 PC, Suunto Instruments, Helsinki), animal activity, and environmental conditions, including weather, visibility, ice type, and ice cover.

Sighting angles were recorded during surveys and were later converted to distance of the animal from the aircraft. When large concentrations of animals were encountered, their occurrence within different "sectors" of a strip transect were noted. Each of those sectors was 0.25 statute mile wide (0.4 km), as follows: A = 0-0.25 mi; B = 0.25-0.5 mi; C = 0.5-0.75 mi; D = >0.75 mi. Since observers could not see directly below the aircraft, sector boundaries were offset to each side of the aircraft (approximately 15°) during flights made in the Grumman Goose. Sector boundaries for all flights were delineated by the clinometer. In this report, density estimates of pinnipeds other than walruses were based upon only those sightings made within the first 0.25 mi strip on each side of the aircraft; total strip width therefore equaled 0.5 mi (0.8 km). For walruses, strip width equaled 1 mi (1.61 km).

Southern Bering Sea Ice Front Survey

The Alaska Department of Fish and Game (ADF&G) surveys were restricted to the ice front (Fig. 3). Their primary purpose was to determine the distribution and relative abundance of spotted seals. Flights were conducted on 8, 9, 11, 17, 19, 20, 21, and 23 April 1976. The aircraft used was the P2V which had a large Plexiglas observation compartment in the nose. A crew of three persons usually occupied this compartment during the surveys; two were primarily observers, but one also recorded. The third person acted as a back-up observer whose function was to determine the proportion of seals not seen by the primary observers, to verify inclusion or omission of animals at the limit of transects, and to replace primary observers when fatigued. On most flights, a primary observer counted on one side of the aircraft for 2 h, then counted on the other side for 2 h, then rested for up to 1 h. Forward, lateral, and downward visibilities from the observation compartment were excellent.

Survey procedures involved use of strip transects 0.5 nmi (0.93 km) wide on each side of the aircraft, for a total strip width of 1 nmi (1.85 km). Angle indicators were mounted on each side of the observation compartment to limit the outer boundaries of the strip. The survey aircraft was equipped with a GNS500. To the extent possible, survey altitude in the P2V was maintained at 91 m. Lower altitudes were flown when necessitated by weather. Flight speed averaged 160 kn.

[11]Reference to trade names does not imply endorsement by any agencies represented by the authors.

Information recorded included species and number of animals sighted, group size, animal activities, ice types, weather, local time, and navigational information. Animal sightings were recorded continuously in 1 min time intervals.

The P2V flight strips on 8, 9, and 11 April were selected at random. Those surveys on 17 and 19 April were along preselected flight lines designed to achieve a replicate, stratified, random sample in the recognized area of highest seal density. Systematic surveys, flown mainly in an east-west direction, covered the southern portion of the ice front on 20 April and the northern part on 21 April.

Western Bering Sea Survey

The Pacific Institute of Fisheries and Oceanography (TINRO) surveys involved extensive flights over the ice-covered regions of north-central and northwestern Bering Sea. Survey lines generally were oriented north-south and covered all ice types from the front to Bering Strait. Surveys were flown on 12-15, 17, 19, and 21-26 April 1976. The aircraft employed was a Soviet UL-14 equipped with standard navigation instruments.

Marine mammals were observed from the left side of the aircraft by a single observer (Fedoseev) viewing through a bubble-type window installed in the compartment aft of the flight deck. This bubble window provided both vertical and horizontal visibility. The observer also was the recorder.

Flight altitude was 200 m, with occasional descents to 100 m. A strip transect equal in width to the altitude of the aircraft was used. The outer limit of the transect was maintained by sighting a 45° angle from the observation window. All animals observed were recorded, but only those animals sighted within the strip were included in the analysis.

Observation periods varied in duration, usually lasting 1 to 1.5 h, followed by a short rest period. Information recorded for each 5-min survey period included start and end time, start and end coordinates, distance covered, transect width, area surveyed, and kind and number of animals sighted. Ice type was recorded by a hydrologist, also on board the aircraft.

Accuracy of the Counts and Identifications

Only the animals sighted on the ice were included in the analyses, since pinnipeds in the water are difficult to identify from aircraft. Because the ability of the observers to sight animals on the ice was recognized as being impaired by fog and snow, the segments of survey strips covered during such periods of poor visibility were routinely deleted from the analyses.

Walruses are easier to see from low-flying aircraft than are any of the other pinnipeds surveyed, but because they tend to congregate on the ice in dense herds, they are more difficult to count. In these surveys, most of the small groups (< 20) were believed to have been counted accurately, but the numbers in the larger groups mostly were estimated in round numbers.

The sightings of ringed seals probably were the least precise because these seals are the smallest and the most shy (i.e., most disturbed by aircraft) of any of the pinnipeds surveyed. Even under the best of conditions, the numbers sighted on the ice in April probably will be only a very small fraction of the numbers present, since many of the animals (particularly females and pups) at that time haul out in lairs under the snow, where they cannot be seen from the air.

Ribbon seals usually react only slightly to the presence of aircraft, frequently remaining on the ice, even when the plane passes

directly overhead. They are easily identified by their characteristic method of locomotion, as well as by their distinctive coloration. During April, most of the ribbon seals sighted on the ice probably are adult females and pups; adult males tend to remain in the water at that time. The pups are more difficult to sight than are the adults because of their small size and white coloration.

Spotted seals also are easily identified by their locomotion, coloration, and the fact that the adults in April generally occur as pairs on the ice, usually with a white-coated pup. These seals are more disturbed by the aircraft than are the ribbon seals, hence tend to move more rapidly and in a straight line to the water. Because of this motion, the pups usually can be seen, despite their small size and coloration.

Bearded seals are readily seen and identified from the air, because of their large size. They usually are not frightened, often remaining on the ice even when the aircraft passes directly over them. Most of those sighted in April probably are subadults, which occur singly, and adult females with pups; adult males tend to be in the water at that time.

Analytical Methods

Data from the TINRO surveys were computer-plotted directly as numbers of animals sighted per 5-min time segment of each transect. Data from the NMFS and ADF&G surveys were plotted as numbers of animals sighted per 1-min of time within each 10′ × 10′ (0.3 km × 0.3 km) block of latitude and longitude. Where more than one survey strip crossed a 10′ × 10′ (0.3 km × 0.3 km) block, the data were averaged to give equal weight to the survey effort in all blocks.

The data were stratified by the method developed experimentally by Krogman et al. (footnote 10). Estimates of regional density and abundance were computed only from the NMFS surveys by "Method I" of Estes and Gilbert (1978):

$$(1)\ \hat{R} = \Sigma y_i / \Sigma x_i$$

where $\hat{R}$ = density of animals per square nautical mile
y_i = number of animals in the ith survey strip
x_i = area of the ith survey strip

$$(2)\ S^2_{\hat{R}} = \left[\Sigma(y_i^2 / x_i) - \hat{R}\Sigma y_i\right] / (n-1)\,(\Sigma x_i)$$

where $S^2_{\hat{R}}$ = variance of $\hat{R}$
n = number of survey strips

$$(3)\ \hat{T}_y = \hat{R}A$$

where $\hat{T}_y$ = animal abundance in stratum
A = total area of stratum

$$(4)\ V(\hat{T}_y) = A(A - \Sigma x_i)S^2_{\hat{R}}$$

where $V(\hat{T}_y)$ = variance of $\hat{T}_y$.

Average group size was calculated as:

$$(5)\ \overline{G} = \Sigma y_i / \Sigma O_i$$

where $\overline{G}$ = average group size in stratum
O_i = number of observations (= groups in the ith survey strip)

$$(6)\ S^2 = \Sigma(y_i - \overline{G})^2 / \Sigma O_i - 1$$

where S^2 = group size variance.

Abundance estimates with 95% confidence intervals were generated for each region covered by the NMFS surveys. Confidence intervals were calculated as:

$$(7)\ \hat{T} \pm t_{.05(2)V}\ \sqrt{V(\hat{T})}.$$

The notation $t_{.05(2)V}$ refers to the critical value of t where alpha (α) = .05 ($1-\alpha$ = .95) based upon a two-tailed test with V degrees of freedom. Degrees of freedom were calculated as the total number of survey strips minus the number of strata.

RESULTS

Walruses

In the northern Bering Sea, walruses were concentrated to the west and north of St. Lawrence Island, in a pattern suggesting movement through Anadyr Strait (between St. Lawrence Island and the Chukchi Peninsula), toward Bering Strait (Figs. 4, 5). The numbers north of St. Lawrence Island apparently were greater than had been reported previously in this month by Kenyon (footnotes 5, 6). Kenyon's April surveys showed the highest concentrations in this region to be southwest of St. Lawrence Island and in Anadyr Strait. The overall density of animals in the St. Lawrence Island area in April 1976 was 2.77±0.77 (mean ± SD) individuals/nmi² (Table 1, unstratified estimate). Data from the TINRO surveys in that area suggest that the abundance estimate from the NMFS surveys of 25,320±9,744 (mean ± 95% confidence interval) animals was conservative (Krogman et al. footnote 10).

Walruses were conspicuously absent in the central Bering Sea from lat. 59° to 63°N, as well as in Norton Sound and north of lat. 65°N. The ice in those areas was considerably more compact than it was to the north and west of St. Lawrence Island and in Bristol Bay.

Walruses were found in the southeastern part of the Bering Sea, particularly from the Pribilof Islands to Bristol Bay. Highest densities were found 1) around the Pribilof Islands, 2) east of the Pribilofs, approximately 10-40 km north of the ice front, 3) southwest of Cape Newenham, and 4) in outer Bristol Bay (Figs. 4, 6). Walruses were nearly absent from inner Bristol Bay, including Round Island, a traditional summer haulout site. Densities also were lower along the ice front than deeper in the pack, indicating that walruses prefer the heavier pack.

Walruses were most dispersed in Bristol Bay (Table 2) than near St. Lawrence Island (Table 1). The density estimate (unstratified) for Bristol Bay was 0.82±0.22 animals/nmi². An abundance estimate of 30,358±13,933 (95% CI) was derived from the NMFS survey area (Table 2), to which an additional 1,319 animals should be added for the areas covered exclusively by the ADF&G surveys (Krogman et al. footnote 10).

Ringed Seals

In the northern Bering Sea, ringed seals were found to be most closely associated with shorefast and dense pack ice, except just west of St. Lawrence Island (Figs. 7, 8). Along the Soviet coast, they were most abundant in the ice of the eastern Chukchi Peninsula and were numerous also in the southwestern Anadyr ice massif, where the pack ice is characteristically very dense, and in

Table 1.—Walrus statistics from NMFS aerial surveys conducted 13-23 April 1976 in northern Bering Sea. Data were treated by stratified and unstratified methods.

Density stratum	Stratum[1] area (nmi²)	Percent of area sampled	No. of transects	No. of walruses counted			Average group size		Groups/nmi²		Estimated total/stratum	
				Total	Individuals per nmi²	Variance	Animals per group	Variance	No. groups	Variance	No. of walruses	Variance (× 10⁶)
1	6,683	5.00	12	32	0.10	>0.00	6.40	21.71	0.03	>0.00	641	0.12
2	394	14.57	6	12	0.21	0.01	3.00	1.83	0.07	>0.00	82	>0.00
3	315	19.28	3	66	1.09	0.59	4.13	3.03	0.26	0.03	342	0.05
4	3,945	10.90	13	698	1.62	0.20	8.13	3.12	0.20	>0.00	6,401	2.74
5	1,343	5.44	3	267	3.66	0.82	20.54	124.92	0.18	>0.00	4,908	1.40
6	133	14.63	2	254	13.09	195.59	18.14	88.27	0.72	0.45	1,736	2.94
7	86	8.69	2	250	33.30	1,102.89	125.00	625.00	0.27	0.07	2,876	7.51
8	44	17.40	2	451	59.39	3,522.23	56.37	1,765.64	1.05	1.11	2,592	5.54
9	87	13.06	3	750	65.69	425.86	83.33	600.00	0.79	0.07	5,742	2.83
Total stratified	13,030		46	2,780							25,320	23.13
Unstratified	12,878	7.80	17	2,780	2.77	0.60	17.94	12.05	0.15	>0.00	35,622	91.96

[1]Areas were approximated by straight line integration, thus minor discrepancies exist between sum of strata and total unstratified region.

Table 2.—Walrus statistics from NMFS aerial surveys conducted 6-15 April 1976 in southeastern Bering Sea. Data were treated by stratified and unstratified methods.

Density stratum	Stratum[1] area (nmi²)	Percent of area sampled	No. of transects	No. of walruses counted			Average group size		Groups/nmi²		Estimated total/stratum	
				Total	Individuals per nmi²	Variance	Animals per group	Variance	No. groups	Variance	No. of walruses	Variance (× 10⁶)
1	1,472	5.32	3	0	0.00	0.00	—	—	0.00	0.00	0	—
2	1,772	5.62	7	1	0.01	>0.00	1.00	—	>0.00	—	18	>0.00
3	8,037	6.27	15	13	0.03	>0.00	1.86	0.31	0.01	>0.00	207	0.00
4	18,063	8.82	37	298	0.19	>0.00	5.05	1.83	0.04	>0.00	3,378	1.54
5	3,895	14.09	36	712	1.30	0.06	3.61	0.21	0.36	>0.00	5,054	0.81
6	652	9.67	4	124	1.97	0.65	2.70	0.18	0.73	0.07	1,282	0.25
7	272	6.97	2	81	4.28	13.20	4.05	1.38	1.06	2.15	1,163	0.91
8	556	5.02	2	273	9.80	46.46	21.00	120.21	0.47	0.05	5,441	13.64
9	370	6.22	2	302	13.12	37.72	20.13	73.20	0.65	0.05	4,854	4.84
10	167	8.71	2	344	23.99	284.42	10.42	35.85	2.30	0.78	3,947	7.03
11	110	5.78	2	290	45.72	1,791.73	18.13	27.59	2.52	5.45	5,014	20.30
Total stratified	35,364		112	2,438							30,358	49.32
Unstratified	35,230	8.40	32	2,438	0.82	0.05	5.99	0.63	0.14	>0.00	29,014	58.80

[1]Areas were approximated by straight line integration, thus minor discrepancies exist between sum of strata and total unstratified region.

Karaginskii Gulf (Fig. 8). Ringed seals were not numerous offshore, except to the west of St. Lawrence Island (Fig. 7), where many were seen in a rather narrow band associated with thin ice. The mean group size (± 95% CI) north of lat. 60°N was 1.20±0.08 (Table 3).

In southeastern Bering Sea, ringed seals were present from north of the Pribilof Islands to outer Bristol Bay, mainly well north of the ice front (Figs. 7, 8, 9). Densities were low and group size south of lat. 60°N was 1.04±0.02 (Table 3). Those seen 15 to 50 km offshore probably were immature or nonbreeding animals. These animals probably move southward with the advancing pack ice in late winter, away from the preferred breeding habitat in the north.

Ribbon Seals

Apparently, ribbon seals were absent north of lat. 61°N, except in one location southwest of St. Lawrence Island (Figs. 10, 11) but were abundant from the Pribilof Islands west to Olyutorskii Bay (Fig. 12). Most of these were situated from the ice edge to about 100 km north. The distribution appears to have been continuous, with

Table 3.—Comparative statistics for ribbon and ringed seals from NMFS aerial surveys conducted 6-23 April in northern and southeastern Bering Sea.

Species and stratum	Stratum area (nmi²)	Percent of area sampled	No. of transects	No. of seals counted			Average group size		Groups/nmi²		Estimated total/stratum	
				Total	Individuals per nmi²	Variance	Seals per group	Variance	No. groups	Variance	No. of seals	Variance
Ribbon seals, southeastern	35,441	4.21	32	9	0.006	>0.00	1.13	0.016	0.005	>0.00	214	5,236
Ribbon seals, northern	13,547	3.76	18	0	0.000	0.00	—	—	—	—	0	0.000
Ringed seals, southeastern	35,441	4.21	32	25	0.017	>0.00	1.04	0.002	0.016	>0.00	594	66,549
Ringed seals, northern	13,547	3.76	18	30	0.059	0.002	1.20	0.040	0.049	0.01	799	326,959

no major clumping of breeding groups into eastern and western segments, as suggested by Fedoseev and Shmakova (footnote 8).

Density estimates generated from the NMFS surveys were extremely low (Table 3). No estimates were generated for areas covered by the ADF&G and TINRO surveys.

Spotted Seals

Although virtually absent from the northern Bering Sea, spotted seals were widely distributed in the ice front from Bristol Bay to Karaginskii Gulf (Figs. 13, 14, 15). The highest densities were in 1) outer Bristol Bay, 2) central Bering Sea from about long. 175°W to 180°, and 3) Karaginskii Gulf. Density estimates (stratified) from the NMFS surveys in the Bristol Bay region ranged from about 0.05 to 6.3 seals/nmi², with a mean (not stratified) of 0.37 ± 0.06 (Table 4). Densities clearly were greatest in the ice front, decreasing northward into the pack ice. Seals collected by Burns (unpubl. data) in the Bristol Bay concentration in March 1976 were principally subadults, suggesting that there is some age-segregation at that time. The larger groups there also included a few harbor seals, which are abundant in the nearshore zone of that area.

Bearded Seals

These seals were nearly ubiquitous in the Bering Sea pack ice but apparently were concentrated in three or four areas: 1) To the west and north of St. Lawrence Island, 2) in southwestern Anadyr Gulf, 3) about 40 to 60 km north of the ice front in the central Bering Sea, and 4) in the area between the Pribilof Islands and Bristol Bay (Figs. 16, 17, 18). A few were sighted also along the Koryak coast and in Karaginskii Gulf. Densities computed from the NMFS surveys were higher in the northern than in the southern areas (Tables 5, 6).

Overall Relative Abundance

As is apparent from the foregoing descriptions of the distribution of each species, the pinnipeds of the Bering Sea pack ice were not uniformly distributed. Each species tended to be most abundant in a slightly to extremely different part of the pack ice than did the others, presumably because of different habitat requirements and, perhaps, interspecific competition for food or space. For walruses, ringed seals, and bearded seals, the centers of abundance were well

Table 4.—Spotted seal statistics from NMFS aerial surveys conducted 6-15 April 1976 in southeastern Bering Sea. Data were treated by stratified and unstratified methods.

Density stratum	Stratum[1] area (nmi²)	Percent of area sampled	No. of transects	No. of spotted seals counted: Total	Individuals per nmi²	Variance ($\times 10^{-3}$)	Average group size: Seals per group	Variance ($\times 10^{-3}$)	Groups/nmi²: No. groups	Variance ($\times 10^{-3}$)	Estimated total/stratum: No. of seals	Variance ($\times 10^{6}$)
1	5,872	3.34	12	9	0.046	0.1	1.50	11.7	0.03	>0.0	269	0.02
2	8,475	4.03	22	18	0.053	>0.0	1.20	1.1	0.04	>0.0	446	0.03
3	14,762	4.02	30	41	0.069	>0.0	1.58	1.6	0.04	>0.0	1,020	0.08
4	382	5.05	3	2	0.121	1.0	1.00	0.0	0.12	1.0	40	>0.00
5	217	17.08	6	7	0.189	0.8	1.40	6.0	0.14	0.4	41	>0.00
6	581	3.41	2	7	0.354	4.8	1.75	22.9	0.20	0.9	206	0.02
7	240	4.55	2	4	0.366	1.7	1.33	11.1	0.28	0.3	88	>0.00
8	214	8.60	4	7	0.380	2.7	1.40	6.0	0.27	1.1	81	>0.00
9	2,530	6.45	19	84	0.515	1.0	1.59	1.0	0.33	0.3	1,302	0.06
10	733	3.74	2	27	0.985	1.0	1.23	0.8	0.80	0.2	722	>0.00
11	108	9.60	4	12	1.161	54.2	2.40	6.0	0.48	7.3	125	>0.00
12	476	2.97	3	27	1.909	106.9	2.08	5.7	0.92	11.2	909	0.24
13	385	3.92	2	54	2.577	241.9	1.46	2.0	2.45	113.6	1,377	0.34
14	666	6.06	8	254	6.290	492.4	4.62	74.6	1.36	15.9	4,190	2.05
Total stratified	35,587		119	553							10,876	2.84
Unstratified	35,441	4.21	32	552	0.370	3.3	2.21	4.4	0.17	0.3	13,125	39.79

[1]Areas were approximated by straight line integration, thus minor discrepancies exist between sum of strata and total unstratified region.

Table 5.—Bearded seal statistics from NMFS aerial surveys conducted 12-23 April 1976 in northern Bering Sea. Data were treated by stratified and unstratified methods.

Density stratum	Stratum[1] area (nmi²)	Percent of area sampled	No. of transects	No. of bearded seals counted: Total	Individuals per nmi²	Variance ($\times 10^{-3}$)	Average group size: Seals per group	Variance ($\times 10^{-3}$)	Groups/nmi²: No. groups	Variance ($\times 10^{-3}$)	Estimated total/stratum: No. of seals	Variance ($\times 10^{3}$)
1	3,580	5.66	18	7	0.035	>0.0	1.00	0.0	0.04	>0.0	124	1.6
2	6,642	2.13	9	11	0.078	0.1	1.10	1.0	0.07	0.1	516	43.3
3	2,738	3.96	8	14	0.129	0.3	1.17	1.3	0.11	0.2	354	26.6
4	189	2.40	2	2	0.440	407.8	1.00	0.0	0.44	407.8	83	142.3
5	43	8.70	2	2	0.537	0.0	1.00	0.0	0.54	0.0	23	0.0
6	221	8.80	2	8	0.822	6.6	2.00	100.0	0.41	1.7	182	3.1
7	86	6.53	3	5	0.893	3.1	1.67	11.1	0.54	0.0	77	0.2
8	131	5.81	3	7	0.918	41.6	1.75	22.9	0.53	13.6	120	6.8
9	129	4.34	2	6	1.067	>0.0	1.50	8.3	0.71	1.6	138	>0.0
10	43	8.70	2	10	2.682	260.2	2.00	10.0	1.34	65.0	115	4.4
Total stratified	13,802		51	72							1,732	228.3
Unstratified	13,547	3.76	18	72	0.141	0.1	1.35	1.0	0.10	>0.0	1,917	186.6

[1]Areas were approximated by straight line integration, thus minor discrepancies exist between sum of strata and total unstratified region.

Table 6.—Bearded seal statistics from NMFS aerial surveys conducted 6-15 April 1976 in southeastern Bering Sea. Data were treated by stratified and unstratified methods.

Density stratum	Stratum[1] area (nmi²)	Percent of area sampled	No. of transects	No. of bearded seals counted			Average group size		Groups/nmi²		Estimated total/stratum	
				Total	Individuals per nmi²	Variance ($\times 10^{-3}$)	Seals per group	Variance ($\times 10^{-3}$)	No. groups	Variance ($\times 10^{-3}$)	No. of seals	Variance ($\times 10^{3}$)
1	14,040	4.07	34	12	0.021	>0.0	1.20	1.8	0.02	>0.0	295	29.4
2	5,974	3.71	27	5	0.023	>0.0	1.00	0.0	0.02	>0.0	135	2.7
3	5,883	3.44	19	5	0.025	>0.0	1.00	0.0	0.03	>0.0	145	5.6
4	4,586	4.15	18	9	0.047	>0.0	1.13	1.6	0.04	>0.0	217	6.6
5	382	11.45	11	4	0.091	0.2	1.00	0.0	0.09	0.2	35	0.3
6	269	14.01	6	6	0.159	0.3	1.20	4.0	0.13	0.2	43	0.2
7	165	5.90	2	2	0.205	4.0	2.00	—	0.10	—	34	1.0
8	1,535	7.40	18	24	0.211	0.3	1.09	0.8	0.19	0.3	324	7.4
9	471	3.87	2	4	0.219	0.7	1.00	0.0	0.22	0.7	103	1.4
10	218	6.34	2	4	0.289	7.4	1.33	11.1	0.22	2.7	63	3.3
11	322	7.28	4	7	0.298	0.4	1.17	2.8	0.26	0.3	96	0.4
12	110	4.98	2	2	0.365	10.3	1.00	0.0	0.37	10.3	40	1.2
13	641	8.19	11	21	0.400	1.5	1.17	0.8	0.34	1.1	256	5.7
14	495	4.35	2	9	0.418	2.2	1.00	0.0	0.42	2.2	207	5.1
15	374	4.35	6	8	0.491	1.1	1.14	2.0	0.43	1.4	184	1.5
16	157	2.91	2	8	1.748	308.4	2.67	277.8	0.66	43.4	275	71.8
Total stratified	35,622		166	130							2,452	145.9
Unstratified	35,441	4.21	32	124	0.083	>0.0	1.16	0.3	0.07	>0.0	2,948	367.6

[1]Areas were approximated by straight line integration, thus minor discrepancies exist between sum of strata and total unstratified region.

inside of the pack ice; those of the ribbon and spotted seals were in the ice front itself.

Within the ice front, the spotted seals showed essentially three centers of abundance, in the southeastern, central, and southwestern sectors, whereas the ribbon seals were centered primarily in the west-central front zone (Fig. 19). In the inner pack ice, walruses were centered in the southeastern and north-central sectors, as had been shown previously by Kenyon (footnotes 5, 6).

The ringed seals were abundant in patches in the southwestern, northern, and southeastern sectors, mainly outside of the areas inhabited by the walruses. Bearded seals were most abundant in the southeastern, central, and northern sectors in and around the areas occupied by both the walruses and the ringed seals.

Compartmenting the surveyed area into six sectors, in which the survey effort was approximately comparable, we find that the ringed and bearded seals and walruses all showed their greatest abundance within the same (north-central) sector, and that both the ribbon and the spotted seal were most abundant in the west-central sector (Table 7). Although walruses and spotted seals were the two most frequently sighted species in the southeastern sector, each was more abundant in another part of the Bering Sea pack ice; similarly, ribbon and ringed seals showed centers of abundance in the southwestern sector, but each was more abundant elsewhere.

Table 7.—Comparative abundance of pinnipeds sighted (no./min.) in relation to location in the Bering Sea pack ice, April 1976.[1]

Pinniped	Sector of pack ice[2]					
	Southeastern	East-central	West-central	Southwestern	North-central	Northwestern
Walrus	1.2-76.0	1.2-8.2	0.2- 1.0	0	0.6-197.5	0.4-1.3
Ringed seal	0.2- 1.6	0.2-0.8	0.2	0.2- 1.0	0.2- 4.4	0.2-0.6
Ribbon seal	0.2- 0.6	0.2-0.9	0.2- 6.0	0.2- 1.2	3.0	0
Spotted seal	0.4-22.0	0.4-7.0	0.4-24.5	0.5-11.9	0	0.4
Bearded seal	0.2- 2.2	0.2-0.9	0.2- 3.0	0.5- 1.0	0.2- 5.0	0.2-3.0

[1]Data from all surveys, combined.

[2]Southeastern = long. 160° to 168°W, south of lat. 61°N; East-central = long. 168° to 174°W, south of lat. 61°N; West-central = long. 174°W to 176°E, south of lat. 61°N; Southwestern = long. 176° to 162°E; North-central = long. 168° to 176°W, north of lat. 61°N; Northwestern = long. 176°W to 178°E, north of lat. 61°N.

DISCUSSION

The winter pack ice of the Bering Sea is by no means a uniform covering over the water, nor is the marine environment beneath it of uniform physical or biotic composition (Hood and Calder 1981). A wide variety of ice and aquatic habitats is available here, as is indicated by the unusual diversity of marine mammals inhabiting this region (Fay 1974). Because the margin of the ice was exceptionally far south in April 1976, extending to the edge of the continental shelf in the eastern Bering Sea and well beyond it in the west, the variety of habitats available to these mammals was even greater than normal. The partitioning of those habitats among the five species of ice-associated pinnipeds, therefore, probably was about maximal at that time.

The actual densities of pinnipeds in each sector of the ice certainly were greater than could be estimated from the counts along the survey strips, for only the animals that were lying on the ice were included in the computations. At all times, some proportion of the animals is in the water, swimming, feeding, or courting, where only a small proportion of them can be seen from the air. For this reason, each of the estimates of abundance certainly is very conservative, and the degree of conservatism differs greatly between species. For example, the probability is very high that a much lower proportion of the ringed seals than of any other species was on the ice, and a much higher proportion of walruses and spotted seals. Therefore, comparison of estimated densities among the five species within any given region or overall is not a reliable indicator of their relative abundance. Nevertheless, the estimated densities of a given species in different areas probably can be relied on as approximations of that species' relative abundance in each area.

Nearly all of the walruses which were sighted during the several aerial surveys described in this and earlier reports were situated in the north-central sector near St. Lawrence Island, and in the southeastern sector, between Bristol Bay and the Pribilof Islands. During the winter, these are major areas of ice formation and divergence,

where leads and polynyas are plentiful (Burns et al. 1980[12]), and the benthic food supply presumably is adequate. Ringed and bearded seals, like the walruses, also were situated for the most part well north of the southern border of the pack ice, but they were more widely distributed, presumably because of their greater ability to make and maintain breathing holes in even the denser parts of the pack. The distribution of the bearded seals, in general, overlapped those of both the walruses and the ringed seals to a high degree but extended also into a broad sector of the western ice where neither of the other two species was sighted. Earlier, Braham et al. (1977[13]) had indicated that the mean group size of bearded seals in the northern Bering Sea was significantly larger than in the southeastern sector, implying that more of the northern animals were pairs of adults. Reevaluation of those data, however, indicates no difference between sectors.

Most of the ringed seals sighted during our surveys probably were immature or nonbreeding individuals, for the breeding adults in this month (April) mainly inhabit the shorefast ice and haul out only in lairs beneath the drifted snow (Fedoseev 1965; Burns 1970; Smith and Stirling 1975). The presence of these seals in considerable numbers in the southeastern sector of the Bering Sea pack ice is reported here for the first time. Previous information from that region by Kosygin (1966) from shipboard surveys in April 1962 and 1963, indicated that they were absent there. Their regular presence was confirmed, however, by several shipboard sightings from the icebreaker CGC *Glacier* in April 1971 (J. J. Burns, unpubl. data) and by numerous shipboard sightings from the ZRS *Zvyagino* in February-March 1981, during joint Soviet-American investigations of marine mammals.[14]

The predominant inhabitants of the outer 200 km of the pack, all across the Bering Sea, were the ribbon and spotted seals, whose preferred pupping habitat appears to be in the "front" zone, just inside the southern edge of the pack ice (Burns et al. 1972, footnote 12). The front is made up of more or less rectangular floes, about 10 to 20 m in diameter, which are formed from larger fields of ice by the action of sea swells. Ribbon seals were found throughout the front, from Bristol Bay to Karaginskii Gulf, but were most abundant in the west-central sector, over deep waters south of the continental shelf. Spotted seals also were widely distributed in the front but tended to be concentrated only in those parts which were situated over waters about 200 m or less in depth, i.e., along the Koryak-Kamchatka coast, in the central sector, and in southern Bristol Bay. A high proportion of those in Bristol Bay appeared to be immature and nonbreeding animals, with which were mixed a few harbor seals.

Pinnipeds were scarce to absent in the ice over most of the eastern Bering Sea shelf, north of lat. 60°N, as noted in previous surveys by Kenyon (footnotes 5, 6). That region, which comprises most of the inner shelf oceanographic domain, appears to be shunned in part because of its dense, heavy ice cover (McNutt 1981); it may be little used also because of poor secondary production of zooplankton, ichthyoplankton, and benthos on which forage fishes and the pinnipeds themselves might feed (Alton 1974; Motoda and Minoda 1974; Waldron 1981).

[12]Burns, J. J., L. H. Shapiro, and F. H. Fay. 1980. The relationships of marine mammal distributions, densities, and activities to sea ice conditions. Final report, R.U. 248/249, 172 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

[13]Braham, H. W., R. D. Everitt, B. D. Krogman, D. J. Rugh, and D. E. Withrow. 1977. Marine mammals of the Bering Sea: Preliminary analysis of distribution and abundance, 1975-76. Processed rep., 90 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98115.

[14]F. H. Fay, Associate Professor, Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, pers. commun. April 1981.

ACKNOWLEDGMENTS

Robert Everitt participated in all phases of the NMFS surveys and is especially thanked for his significant contributions. Samuel J. Harbo, Jr. assisted in the design of surveys conducted by the ADF&G, and David James participated in all flights. Vitali N. Gol'tsev was an observer during 1 d of the TINRO surveys. National Marine Mammal Laboratory personnel who provided valuable assistance were: Teresa Bray, Clifford Fiscus, Leola Hietala, Richard Punsley, and Ronald Sonntag. We also thank James A. Estes, U.S. Fish and Wildlife Service, and Francis H. Fay, Institute of Marine Science, University of Alaska, for their suggestions and discussions during the initial stages of the research. Appreciation is extended to Douglas G. Chapman, University of Washington, and to Michael F. Tillman, National Marine Mammal Laboratory, for statistical consultation. Ian Stirling contributed valuable suggestions and reviewed the manuscript.

While in Nome we received invaluable assistance from Carl Grauvogel and Ed Muktoyuk, and in King Salmon from Jim Faro and Nick Steen, all with the Alaska Department of Fish and Game. Aircraft logistics for the NMFS and ADF&G surveys were provided by the Office of Aircraft Services, U.S. Fish and Wildlife Service, Anchorage, Alaska.

We also wish to express our gratitude to A. A. Visnevskii, Y. M. Malyshev, and V. F. Omel'chenko, hydrologists from the Kolymsk section of the Hydrometeorological Service, Magadan, USSR, for their help during the TINRO surveys.

Support for the NMFS and ADF&G research came, in part, from contracts administered by the Alaska Outer Continental Shelf Environmental Assessment Program Office, NOAA, Juneau, through an interagency agreement with the Bureau of Land Management, U.S. Department of the Interior.

LITERATURE CITED

ALTON, M. S.
1974. Bering Sea benthos as a food resource for demersal fish populations. *In* D. W. Hood and E. J. Kelley (editors), Oceanography of the Bering Sea, p. 257-277. Institute of Marine Science, Univ. Alaska, Fairbanks.

BELOPOL'SKII, L. O.
1939. On the migrations and ecology of reproduction of the Pacific walrus (*Odobaenus rosmarus divergens* Illiger). Zool. Zh. 18:762-774.

BURNS, J. J.
1970. Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi Seas. J. Mammal. 51:445-454.

BURNS, J. J., G. C. RAY, F. H. FAY, and P. D. SHAUGHNESSY.
1972. Adoption of a strange pup by the ice-inhabiting harbor seal, *Phoca vitulina largha*. J. Mammal. 53:594-598.

EBERHARDT, L. L.
1978. Transect methods for population studies. J. Wildl. Manage. 42:1-31.

ESTES, J. A., and J. R. GILBERT.
1978. Evaluation of an aerial survey of Pacific walruses (*Odobenus rosmarus divergens*). J. Fish. Res. Board Can. 35:1130-1140.

FAY, F. H.
1974. The role of ice in the ecology of marine mammals of the Bering Sea. *In* D. W. Hood and E. J. Kelley (editors), Oceanography of the Bering Sea, p. 383-399. Institute of Marine Science, Univ. Alaska, Fairbanks.
1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North Am. Fauna 74, 279 p. U.S. Fish Wildl. Serv., Washington, D.C.

FEDOSEEV, G. A.
1965. Comparative characteristics of populations of the ringed seal of coastal waters of the Chukchi Peninsula. Izv. TINRO 59:194-212.
1984. Use of nonmetrical characters of skulls of Bering Sea seals in a study of the phenotypic structure of their populations. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:49-54.

HOOD, D. W., and J. A. CALDER (editors).
1981. The eastern Bering Sea shelf: oceanography and resources. Vols. 1 and 2, 1339 p. Univ. Washington Press, Seattle.

JOHNSON, M. L., C. H. FISCUS, B. T. OSTENSON, and M. L. BARBOUR.
1966. Marine mammals. *In* N. J. Wilimovsky and J. N. Wolfe (editors), Environment of the Cape Thompson region, Alaska, p. 877-924. U.S. At. Energy Comm., Wash., D.C.

KOSYGIN, G. M.
1966. Distribution and some features of the biology of pinnipeds of the Bering Sea (spring-summer period, 1963). Izv. TINRO 58:117-124.

KRYLOV, V. I., G. A. FEDOSEEV, and A. P. SHUSTOV.
1964. Pinnipeds of the Far East. Pischevaya Promyshlennost', Moscow, 58 p.

McLAREN, I. A.
1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian arctic. Fish. Res. Board Can., Bull. 118, 97 p.

McNUTT, S. L.
1981. Remote sensing analysis of ice growth and distribution in the eastern Bering Sea. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: oceanography and resources, Vol. 1, p. 141-165. Univ. Washington Press, Seattle.

MOTODA, S., and T. MINODA.
1974. Plankton of the Bering Sea. *In* D. W. Hood and E. J. Kelley (editors), Oceanography of the Bering Sea, p. 207-241. Institute of Marine Science, Univ. Alaska, Fairbanks.

NIKULIN, P. G.
1941. Chukchi walrus. Izv. TINRO 20:21-59.

SHAPIRO, L. H., and J. J. BURNS.
1975. Satellite observations of sea ice movement in the Bering Strait region. *In* G. Weller and S. A. Bowling (editors), Climate of the Arctic, p. 379-386. Geophysical Institute, Univ. Alaska, Fairbanks.

SHUSTOV, A. P.
1965. The distribution of ribbon seal (*Histriophoca fasciata*) in the Bering Sea. *In* E. N. Pavlovskii, B. A. Zenkovich, S. E. Kleinenberg, and K. K. Chapskii (editors), Marine mammals, p. 118-121. Nauka, Moscow.
1969. Test of a quantitative aerovisual survey of seals in the north-western part of the Bering Sea. *In* V. A. Arseniev, B. A. Zenkovich, and K. K. Chapskii (editors), Marine mammals, p. 111-116. Nauka, Moscow.

SMITH, T. G., and I. STIRLING.
1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Can. J. Zool. 53:1297-1305.

TIKHOMIROV, E. A.
1964. On the distribution and biology of pinnipeds of the Bering Sea. *In* P. A. Moiseev, A. G. Kaganovskii, and I. V. Kisevetter (editors), Soviet fisheries investigations in the northeastern part of the Pacific Ocean, Pt. 3, p. 277-285. Pischeveya Promyshlennost', Moscow.
1966a. Identifying the species of Far Eastern seals from an airplane. Izv. TINRO 58:163-172.
1966b. Development and variation of coloration in the pelage of the ribbon seal. Izv. TINRO 58:239-240.

TIKHOMIROV, E. A., and G. M. KOSYGIN.
1966. Prospects for commercial sealing in the Bering Sea. Rybn. Khoz. 42(9):25-28.

WALDRON, K. D.
1981. Ichthyoplankton. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: oceanography and resources, Vol. 1, p. 471-493. Univ. Washington Press, Seattle.

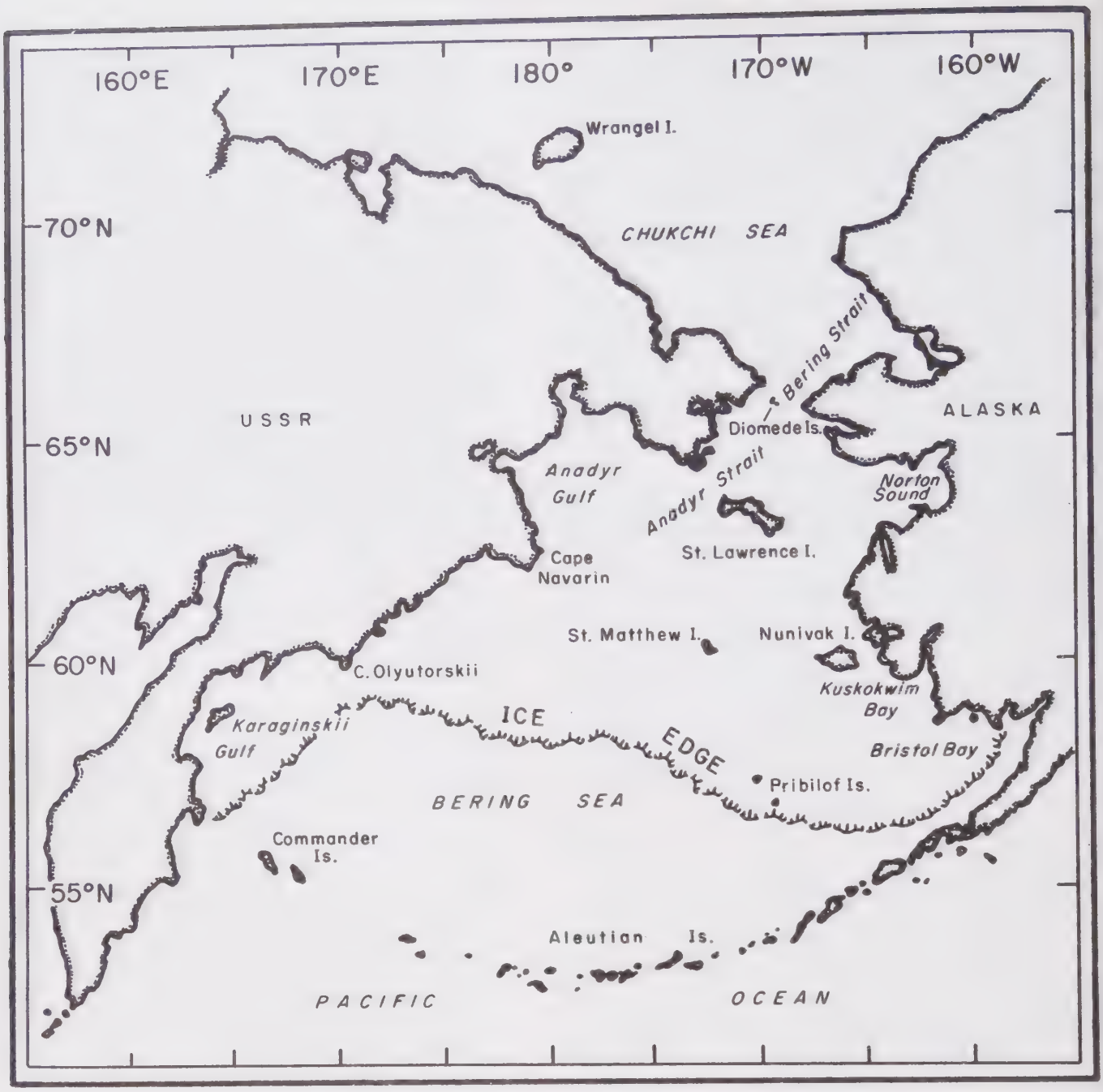


Figure 1.—Study area in which cooperative Soviet-American aerial surveys were conducted. Ice edge is approximate maximum in Bering Sea in April 1976.

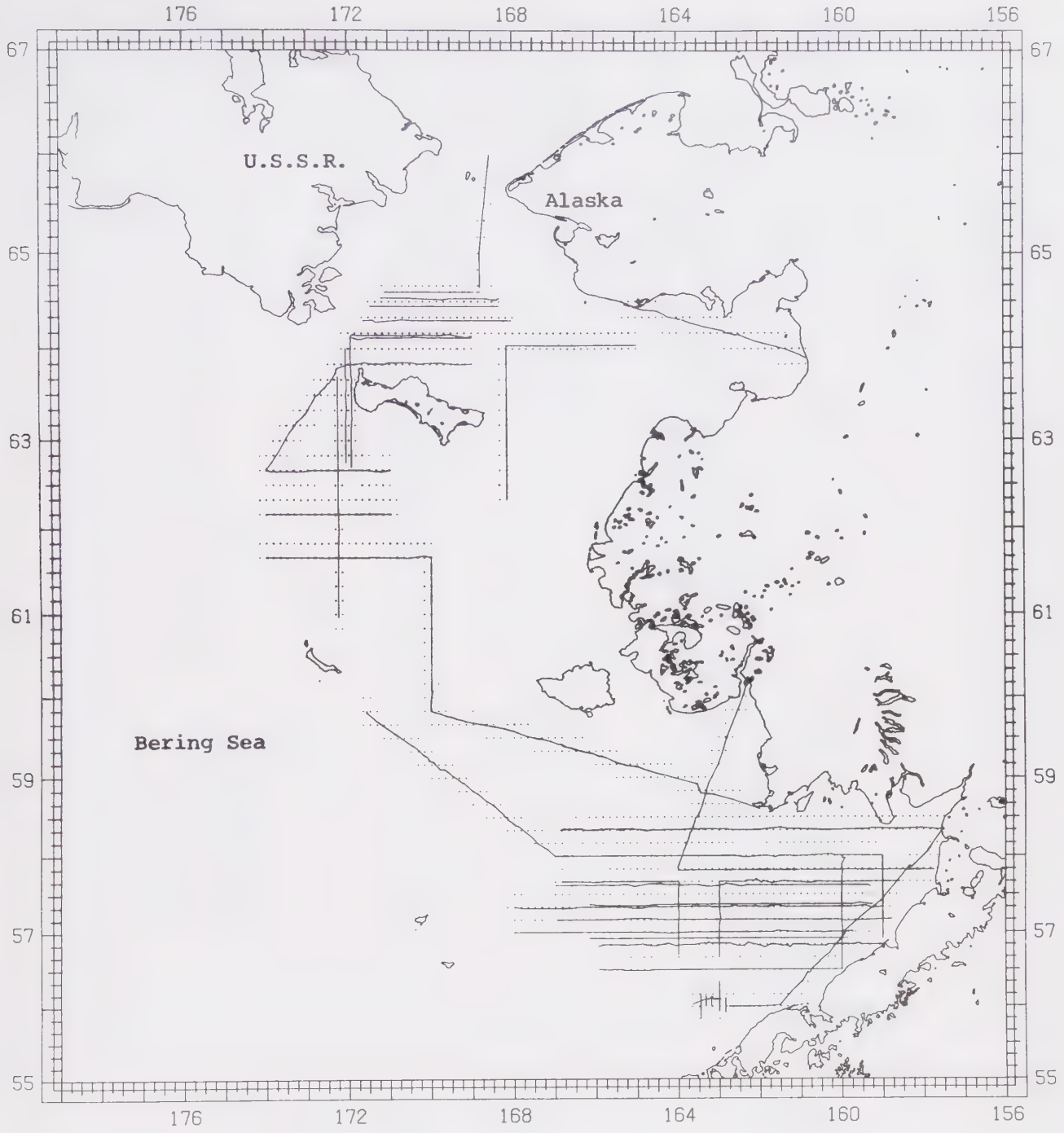


Figure 2.—Computer plot of aerial survey strips flown over eastern Bering Sea by NMFS scientists in April 1976. Dots depict corners of 10 × 10 minute latitude by longitude cells which were overflown by the aircraft.

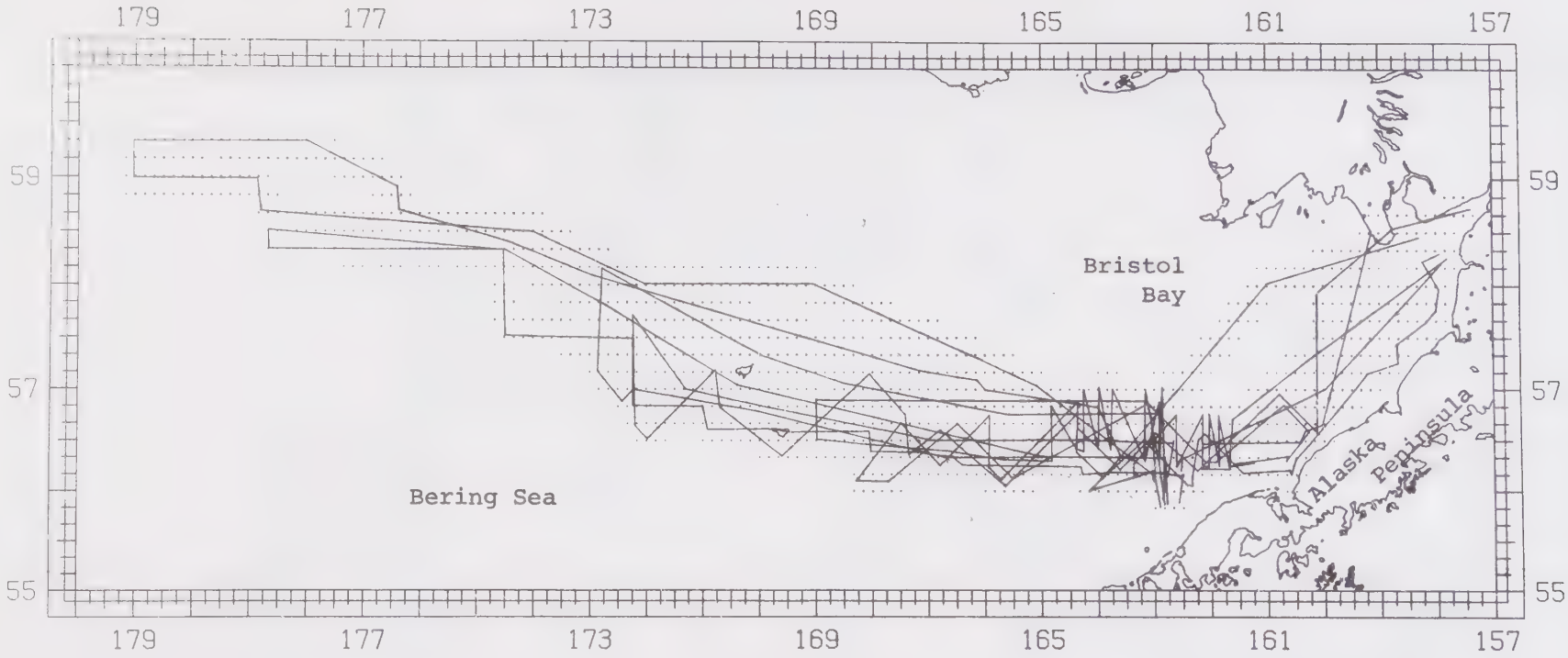


Figure 3.—Computer plot of aerial survey strips flown in southeastern Bering Sea by ADF&G scientists in April 1976. Dots depict corners of 10 × 10 minute latitude by longitude cells which were overflown by the aircraft. The southern limit of surveys marks the southern edge of the pack ice; the northern limit of surveys approximates the inner margin of the ice front.

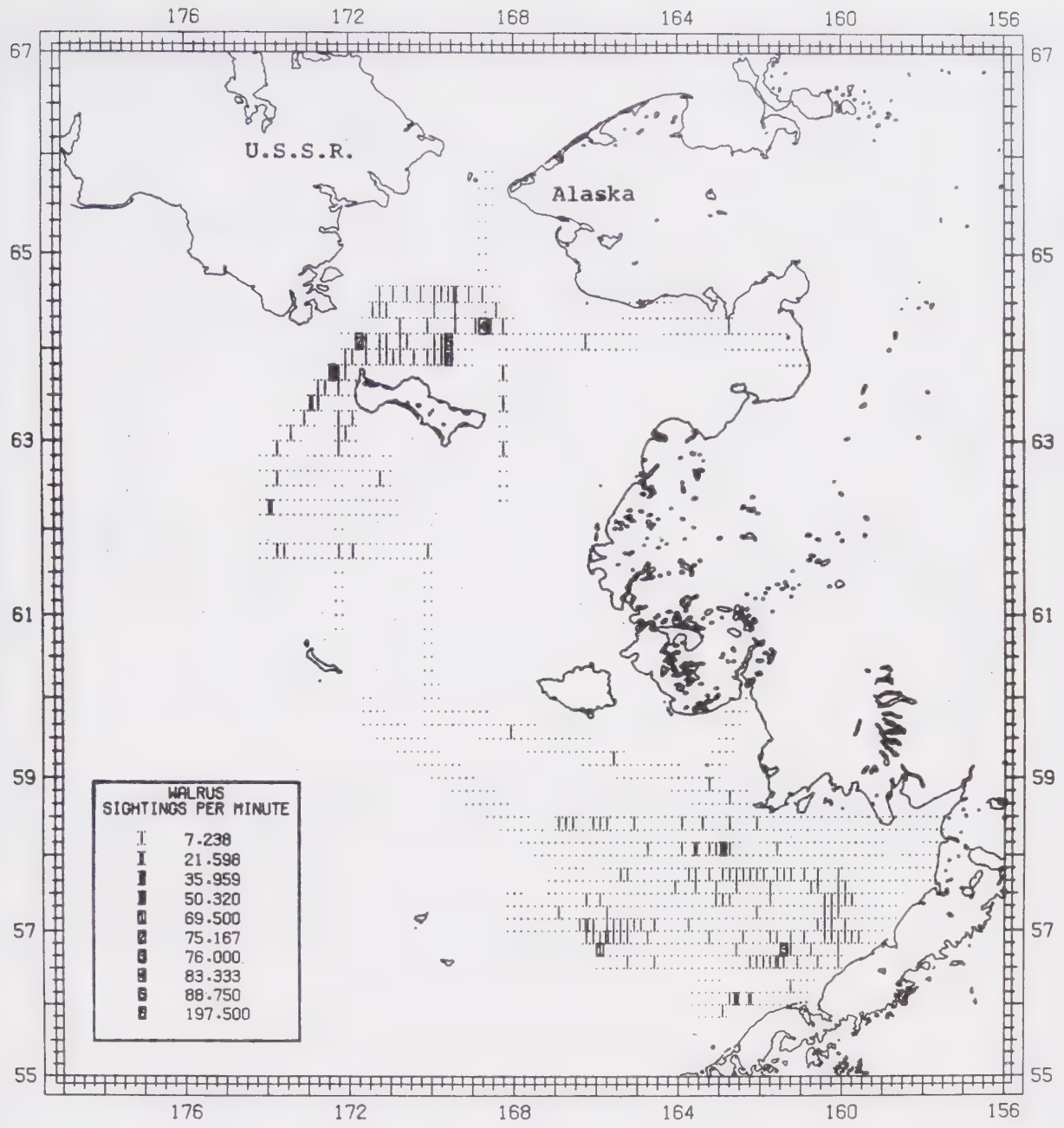


Figure 4.—Computer plots of walrus density from NMFS aerial surveys 6-23 April 1976.

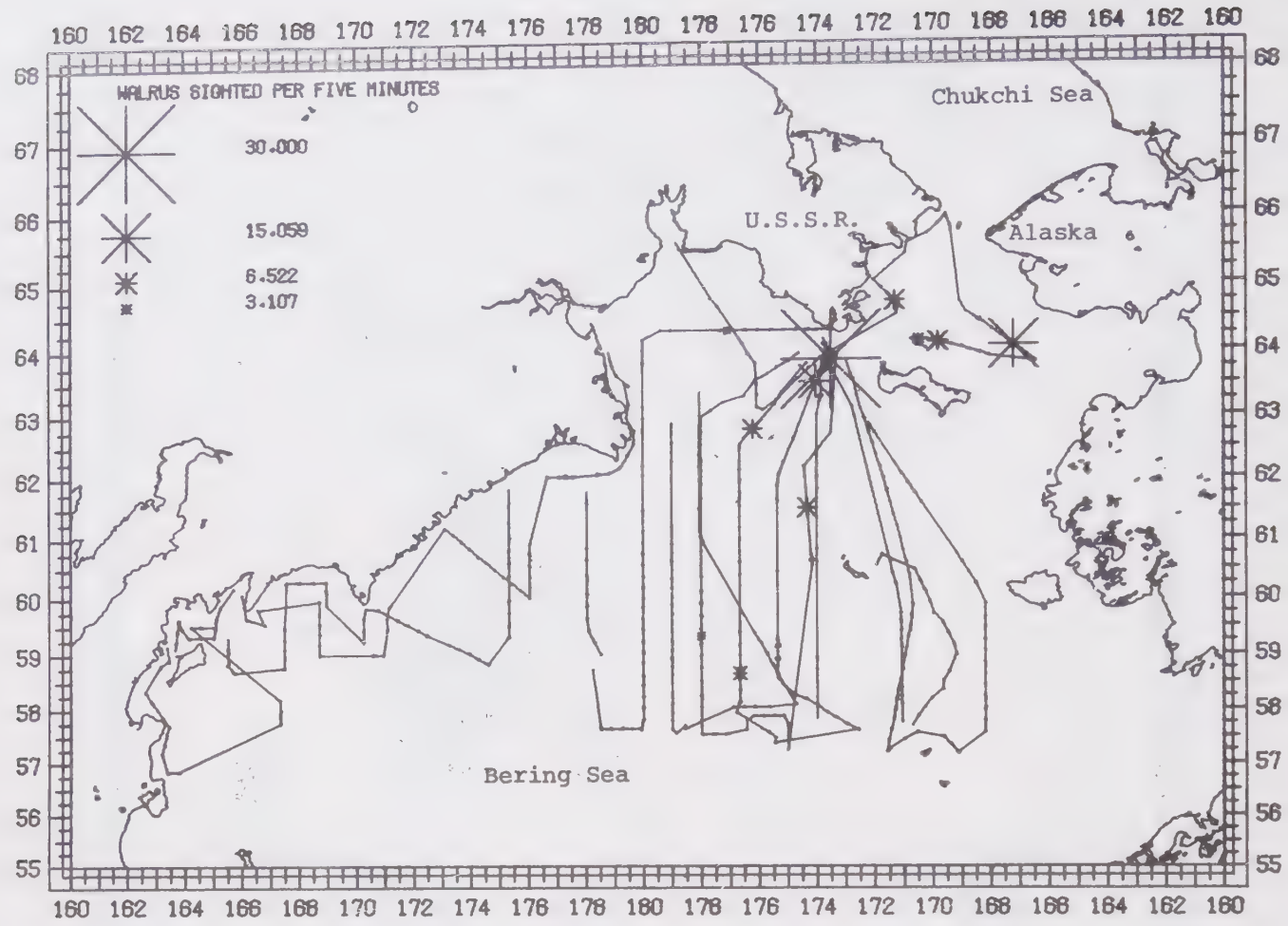


Figure 5.—Computer plots of walrus density in relation to aerial survey strips from TINRO aerial surveys, 12-26 April 1976. Star symbols are centered on positions where walruses were observed.

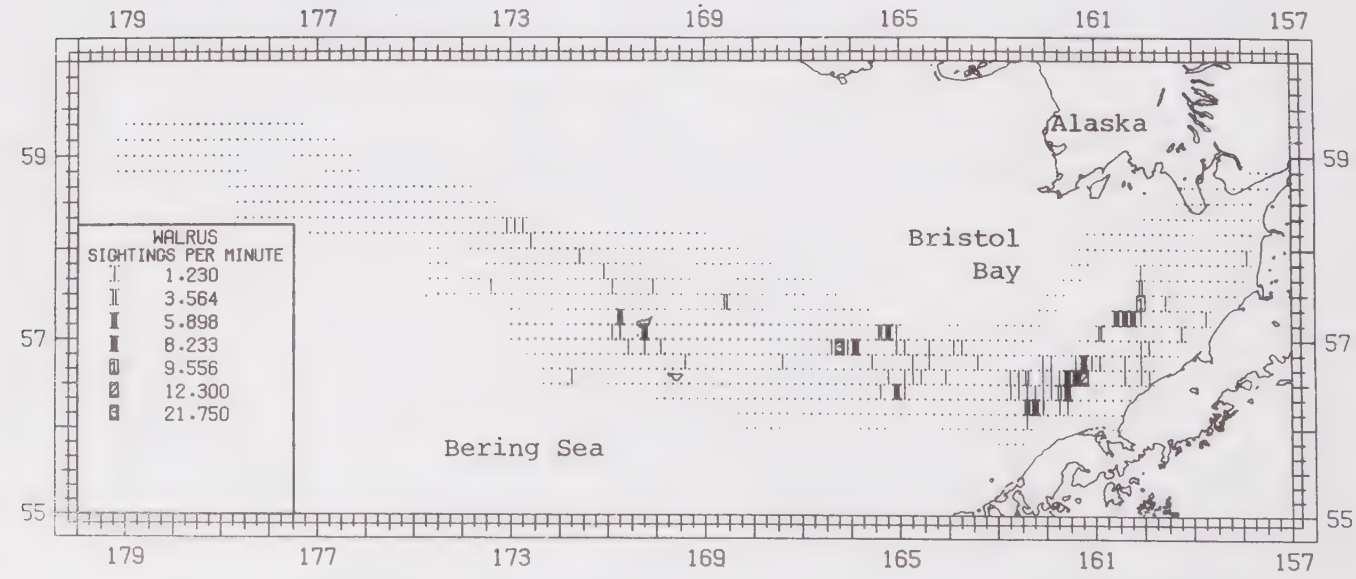


Figure 6.—Computer plots of walrus density from ADF&G aerial surveys, 8-23 April 1976.

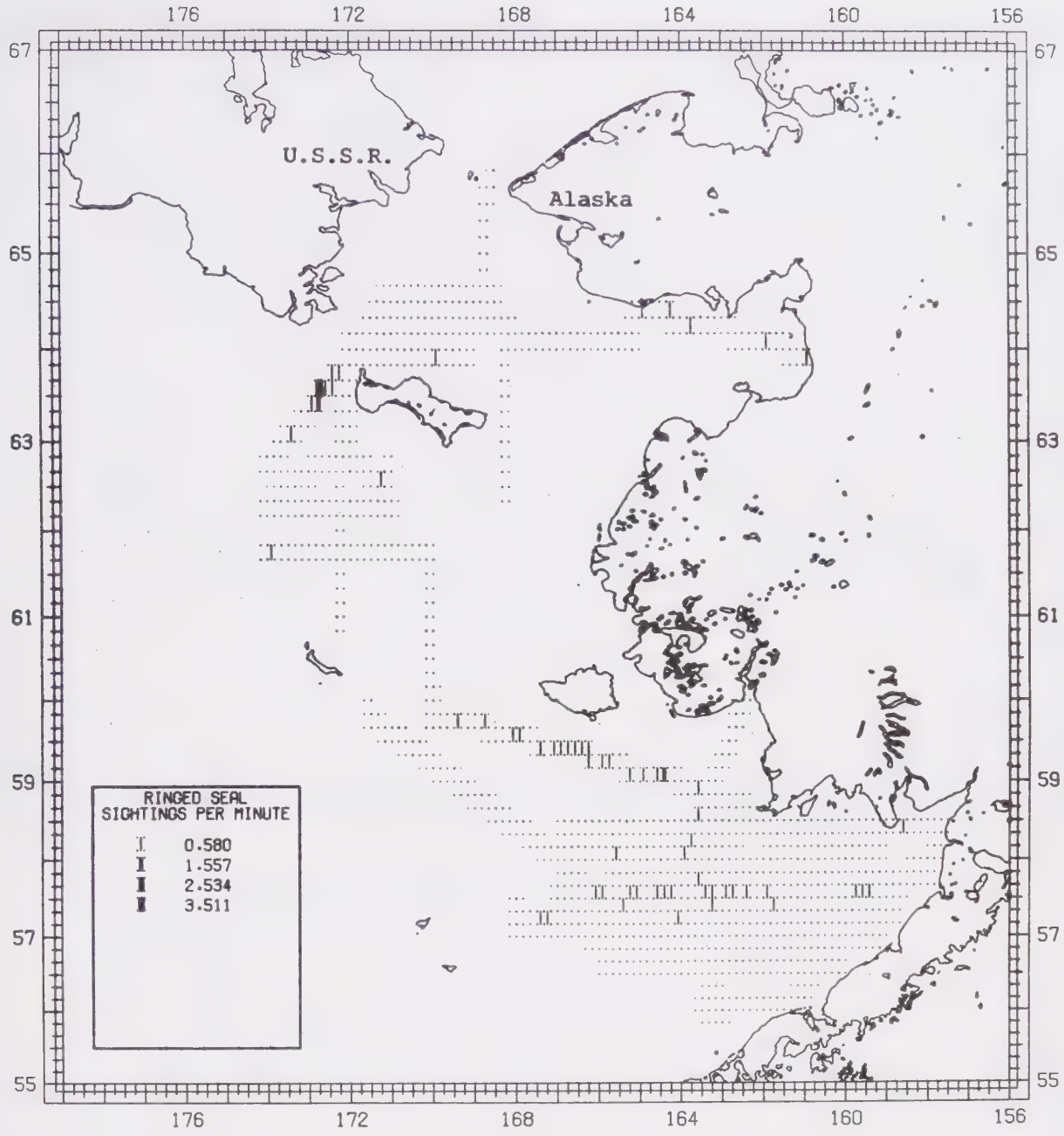


Figure 7.—Computer plots of ringed seal density from NMFS aerial surveys, 6-23 April 1976.

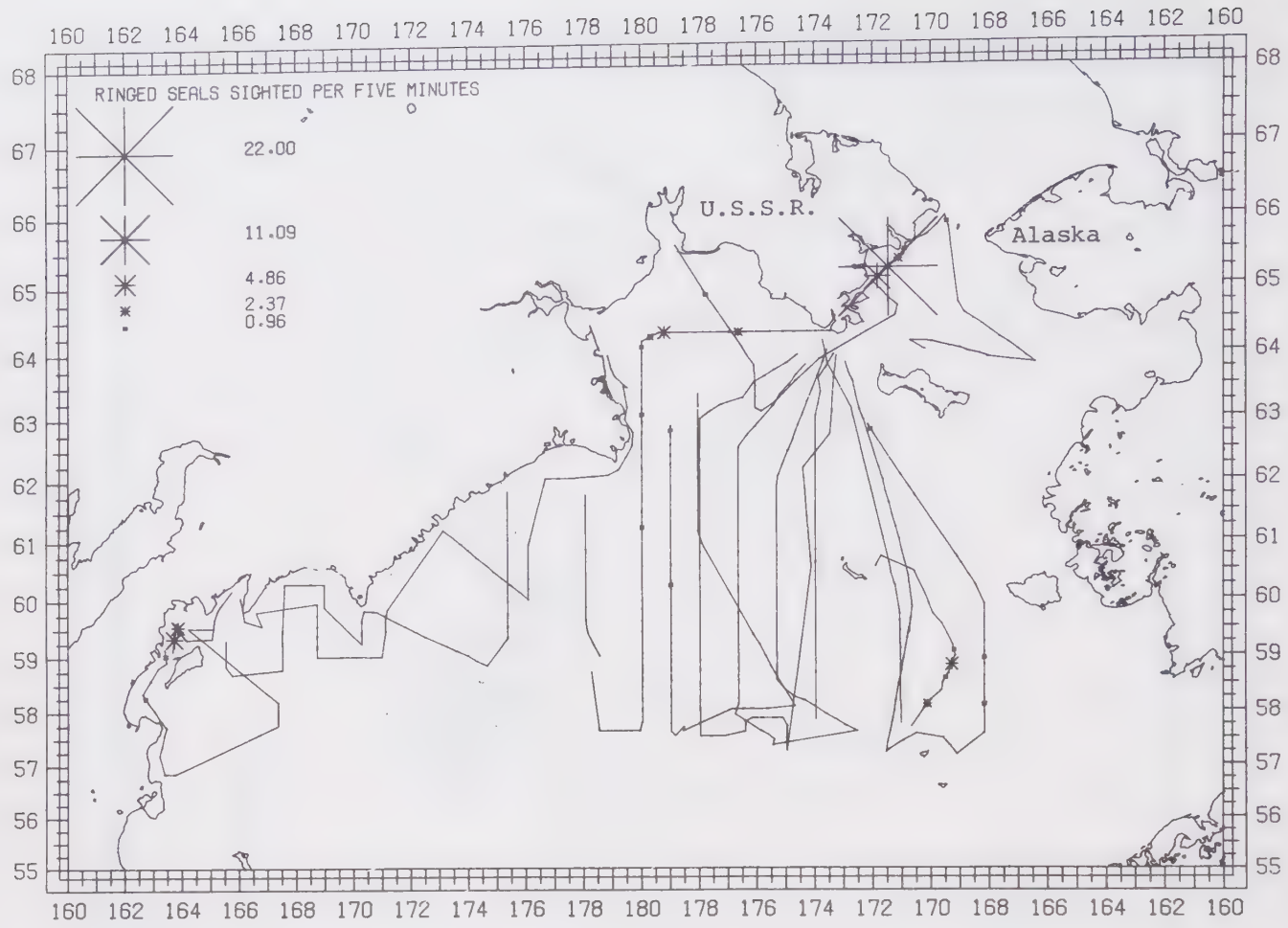


Figure 8.—Computer plot of ringed seal density from TINRO aerial surveys, 12-26 April 1976.

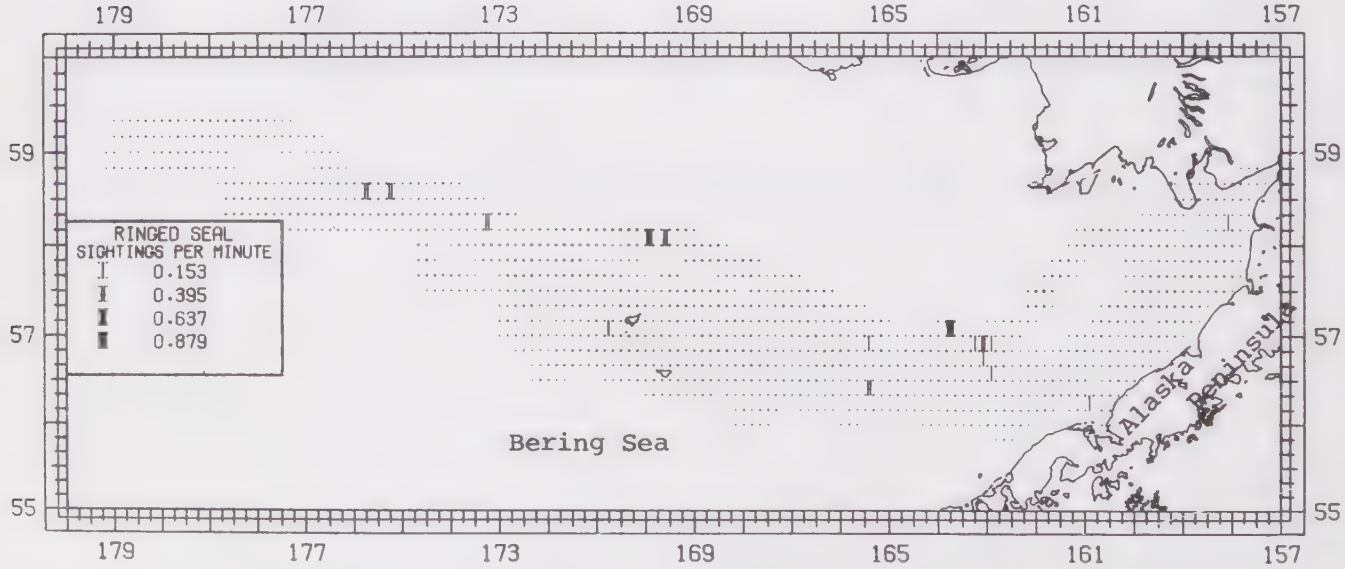


Figure 9.—Computer plot of ringed seal density from ADF&G aerial surveys, 8-23 April 1976.

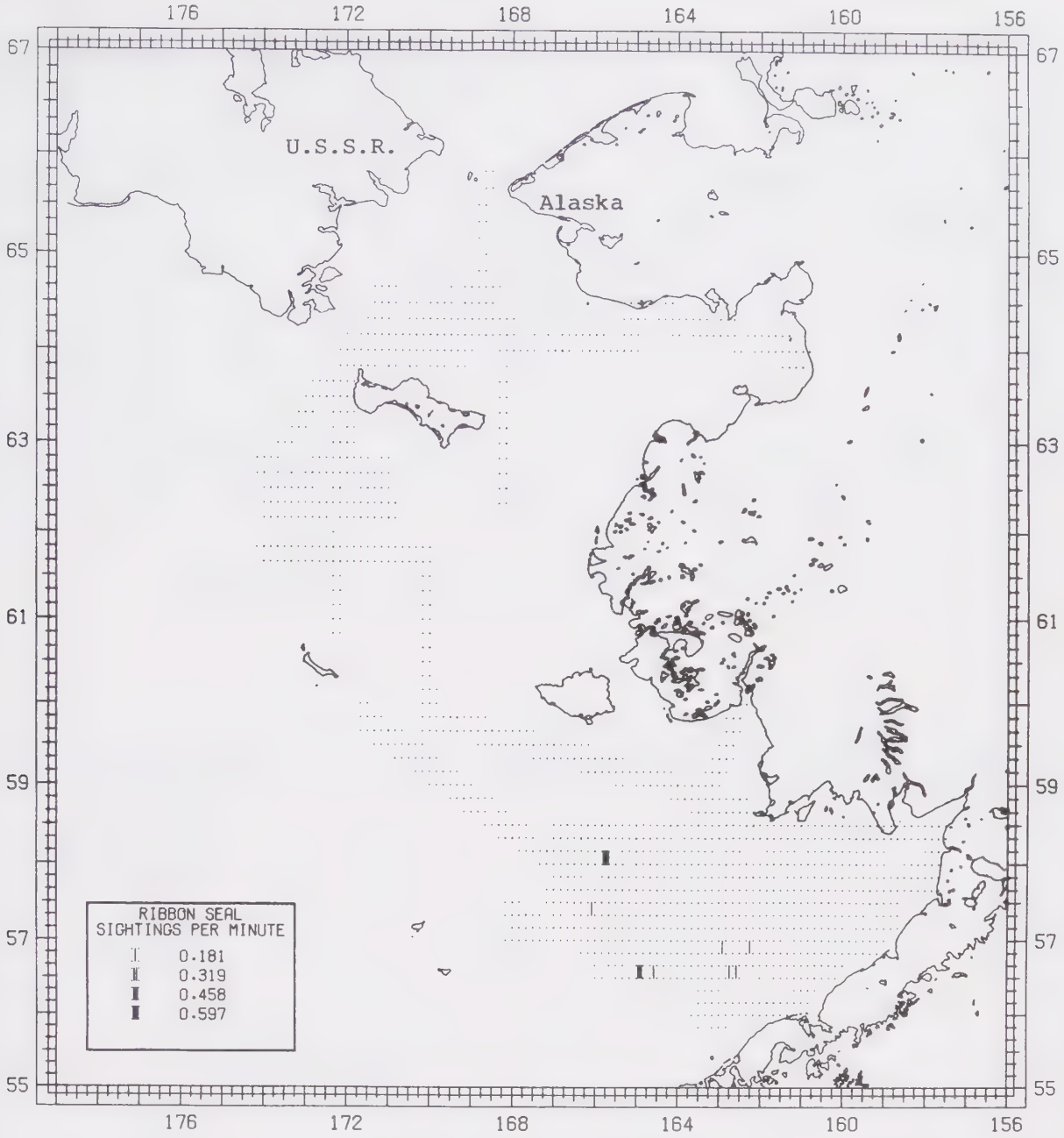


Figure 10.—Computer plot of ribbon seal density from NMFS aerial surveys, 6-23 April 1976.

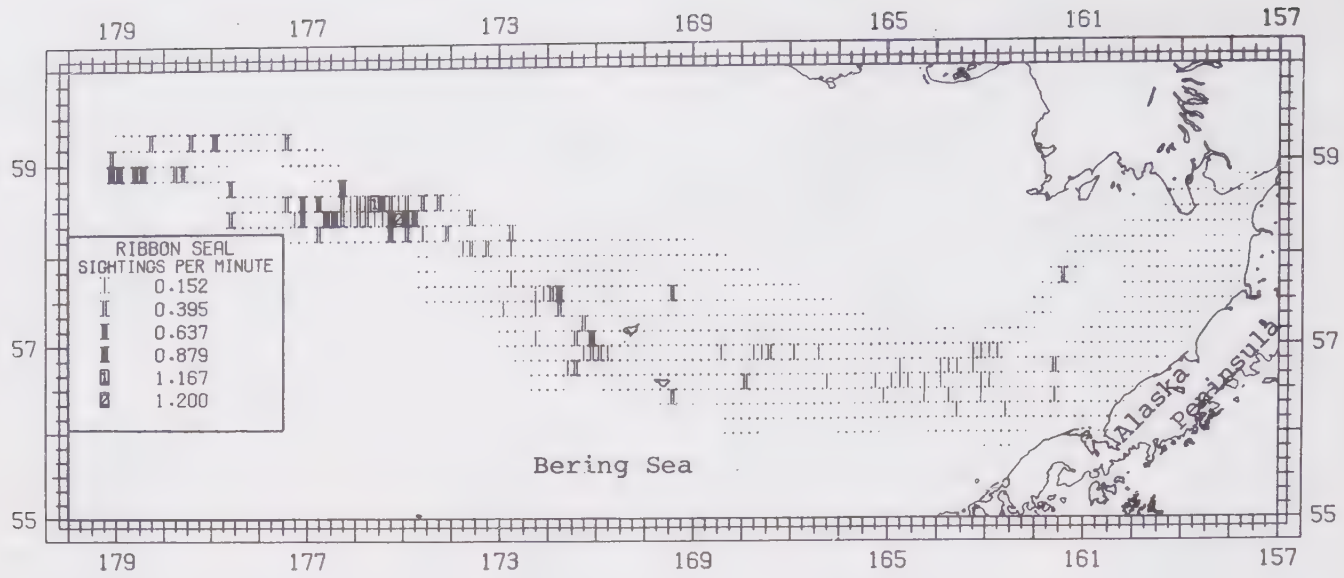


Figure 11.—Computer plot of ribbon seal density from ADF&G aerial surveys, 8-23 April 1976.

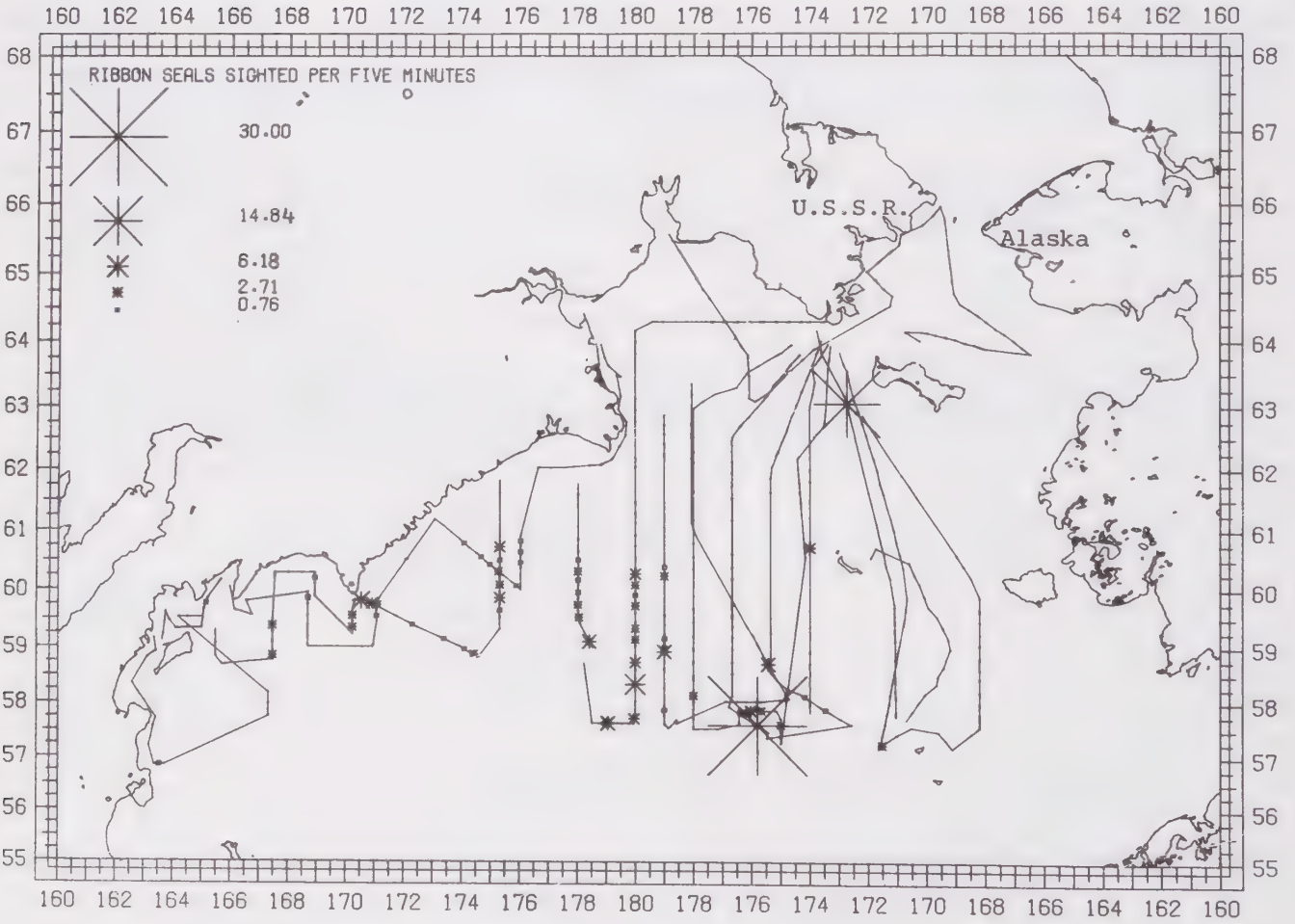


Figure 12.—Computer plot of ribbon seal density from TINRO aerial surveys, 12-26 April 1976.

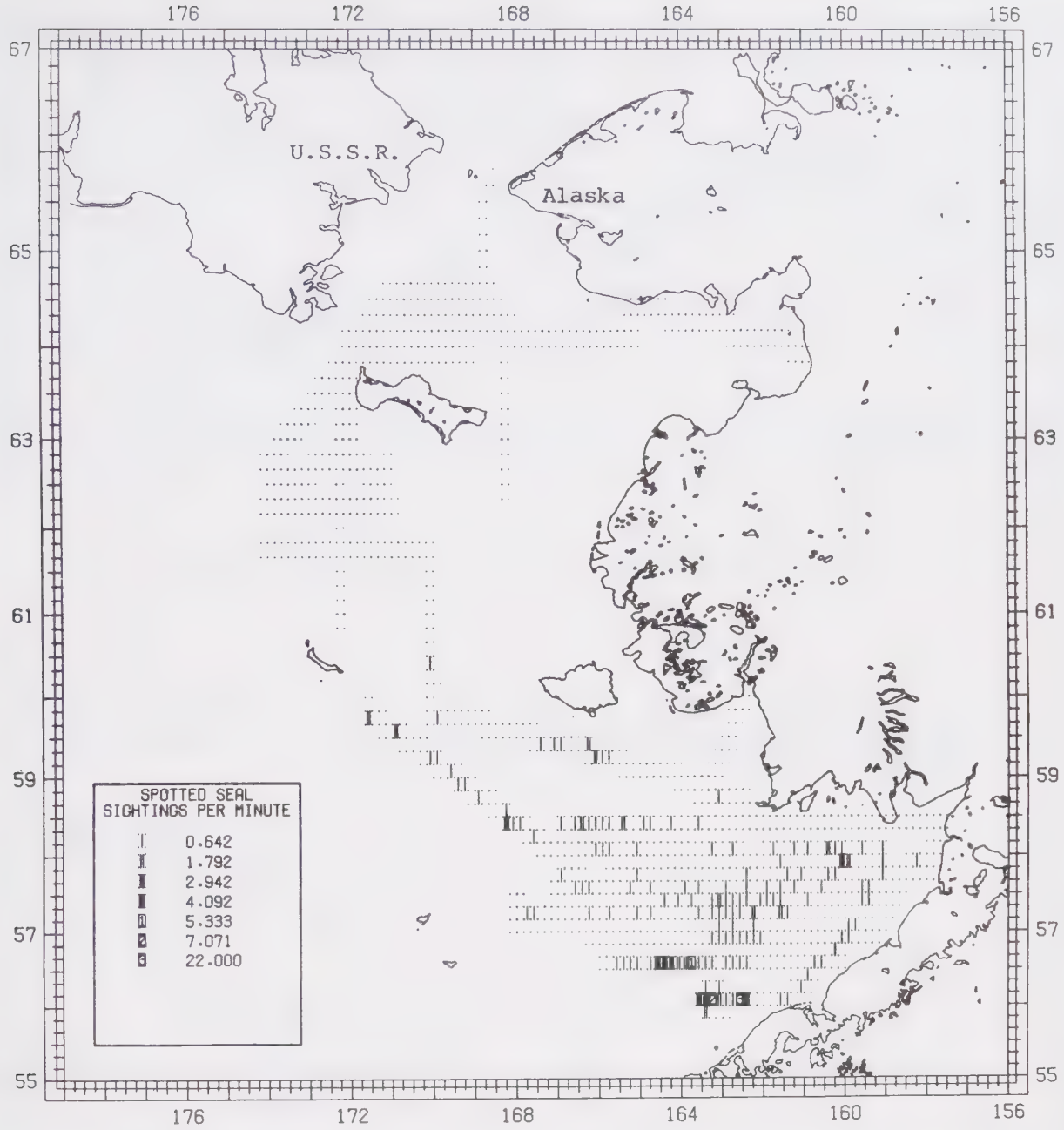


Figure 13.—Computer plot of spotted seal density from NMFS aerial surveys, 6-23 April 1976.

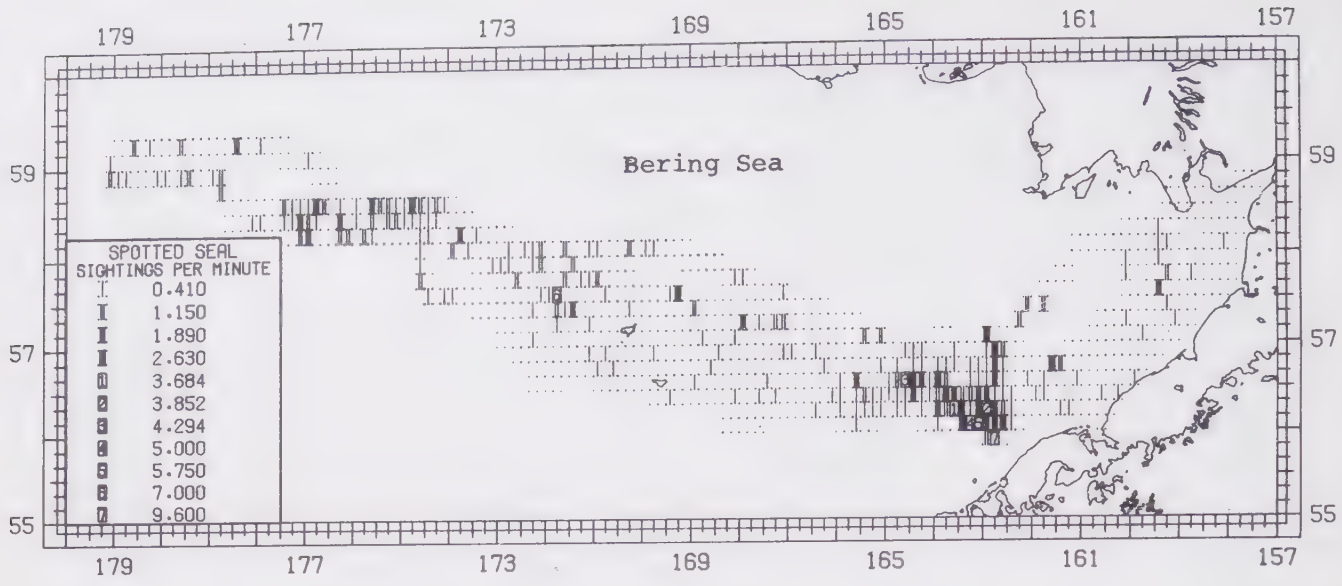


Figure 14.—Computer plot of spotted seal density from ADF&G aerial surveys, 8-23 April 1976.

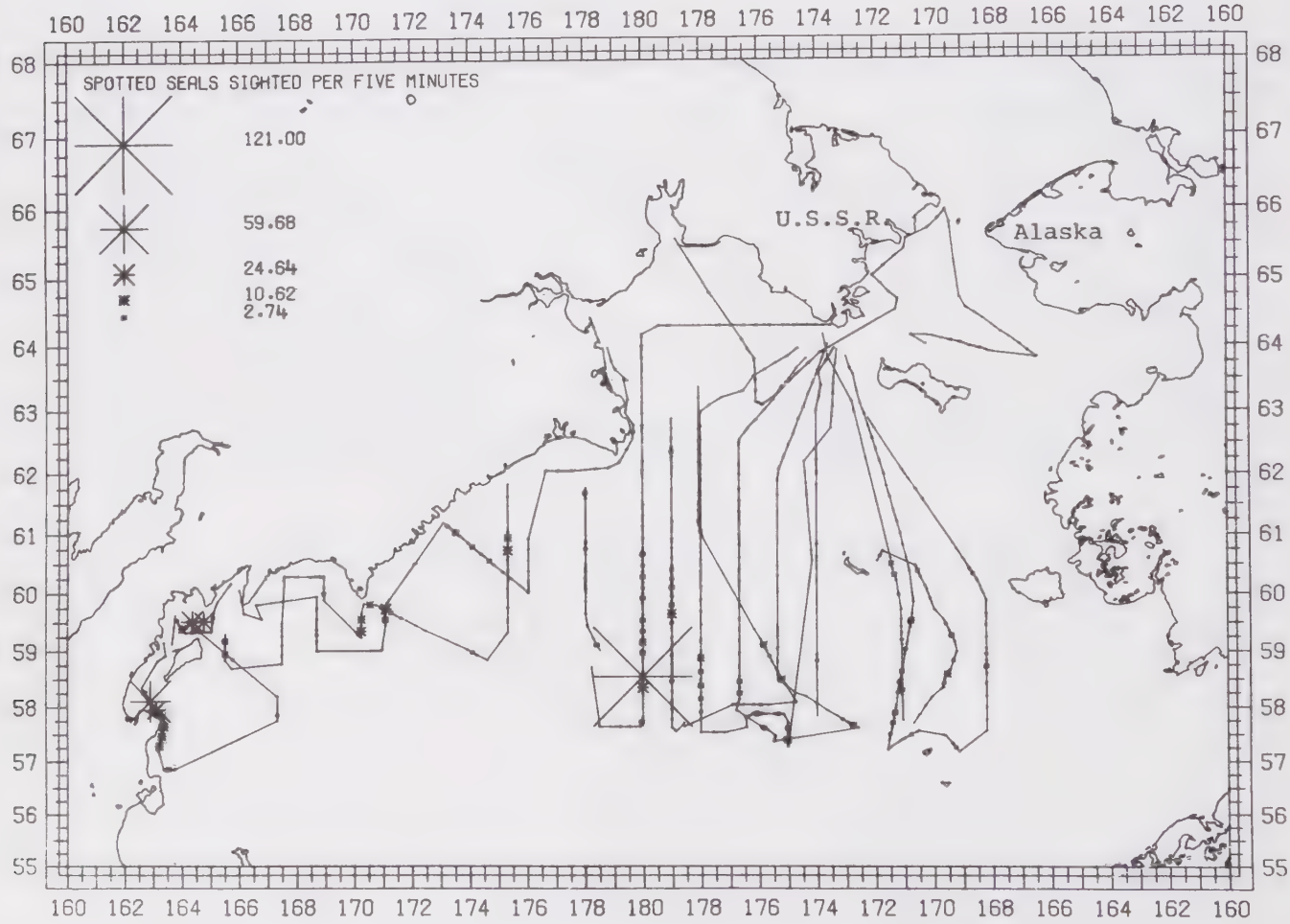


Figure 15.—Computer plot of spotted seal density from TINRO aerial surveys, 12-26 April 1976.

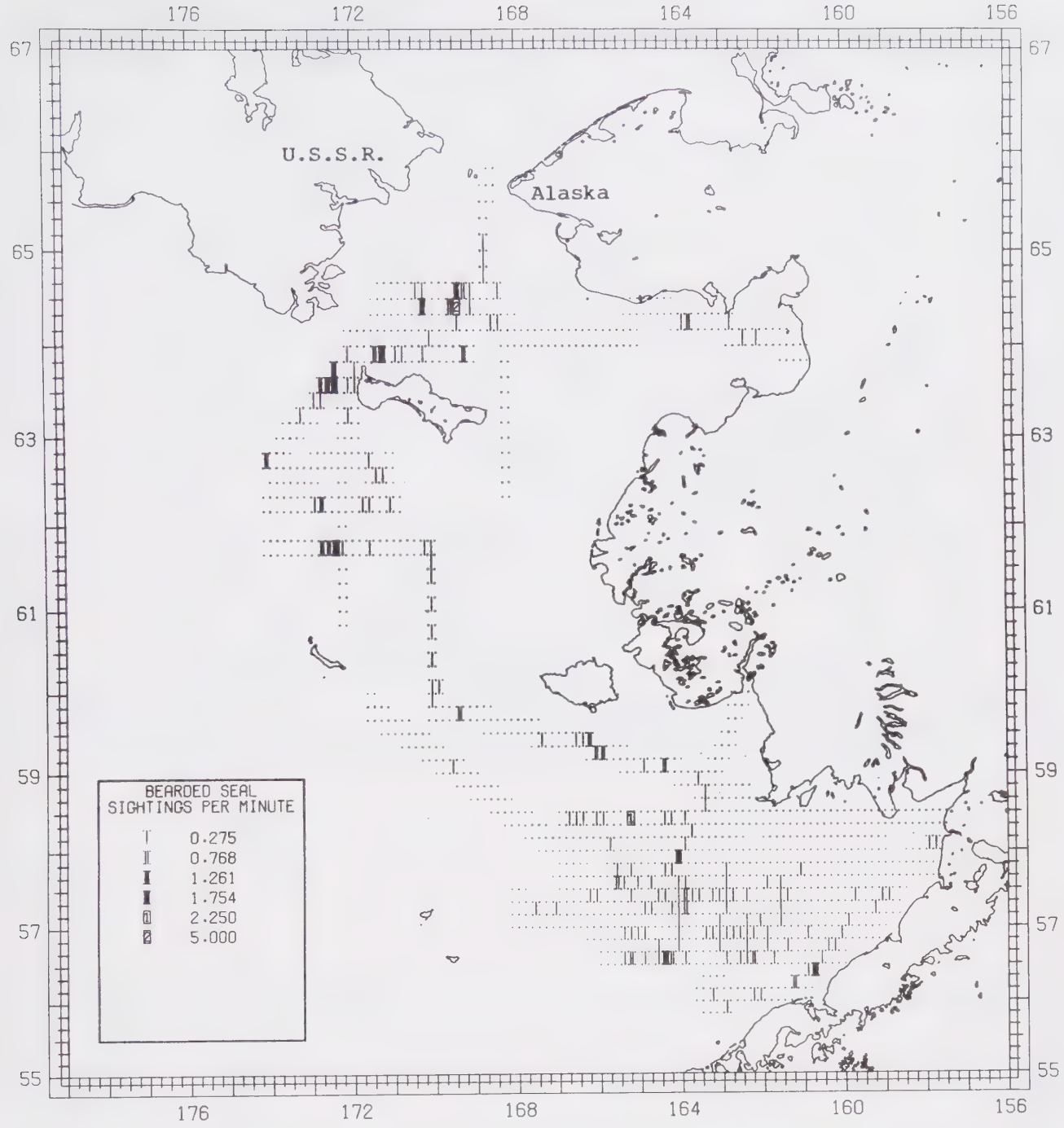


Figure 16.—Computer plot of bearded seal density from NMFS aerial surveys, 6-23 April 1976.

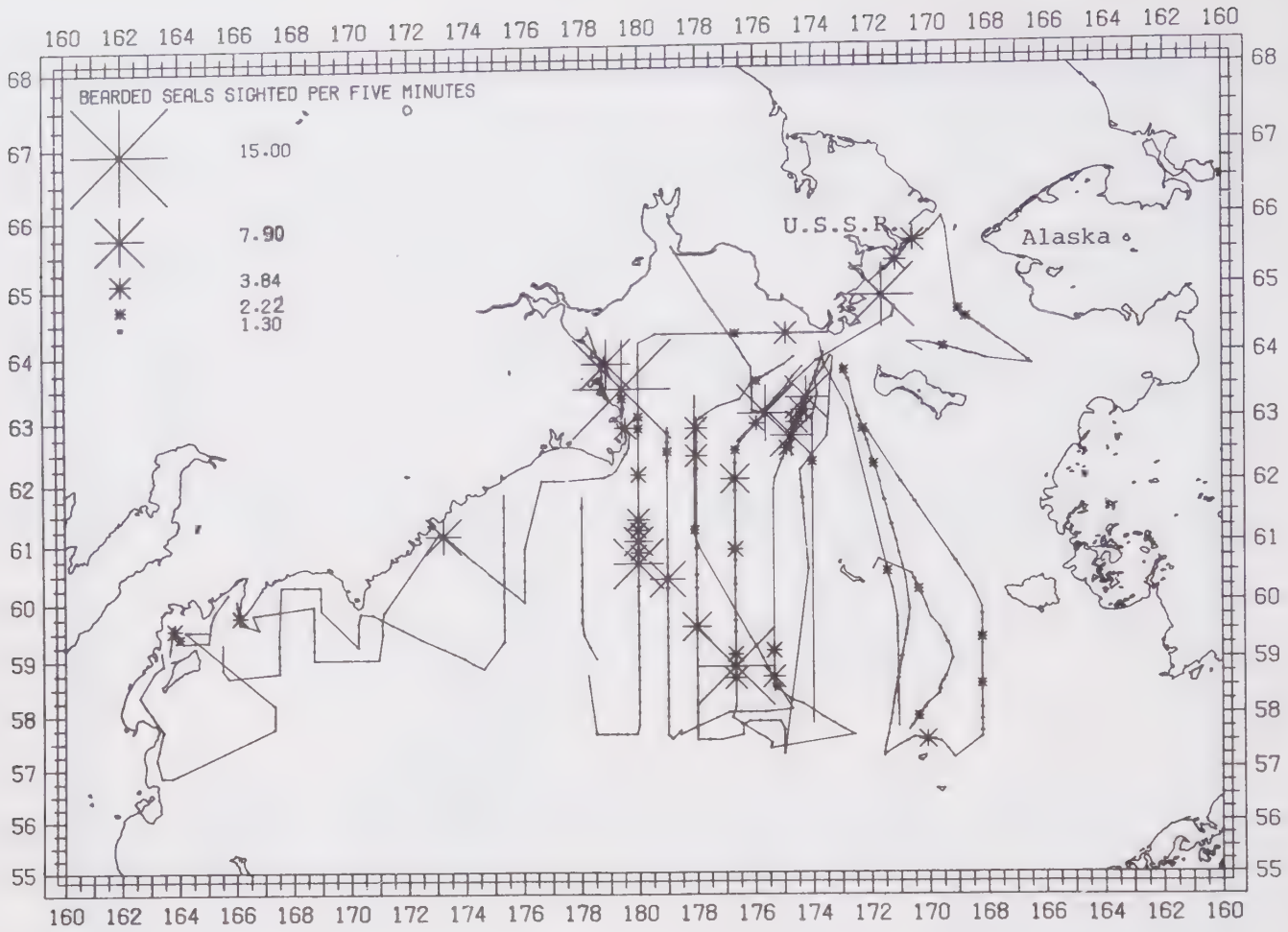


Figure 17.—Computer plot of bearded seal density from TINRO aerial surveys, 12-26 April 1976.

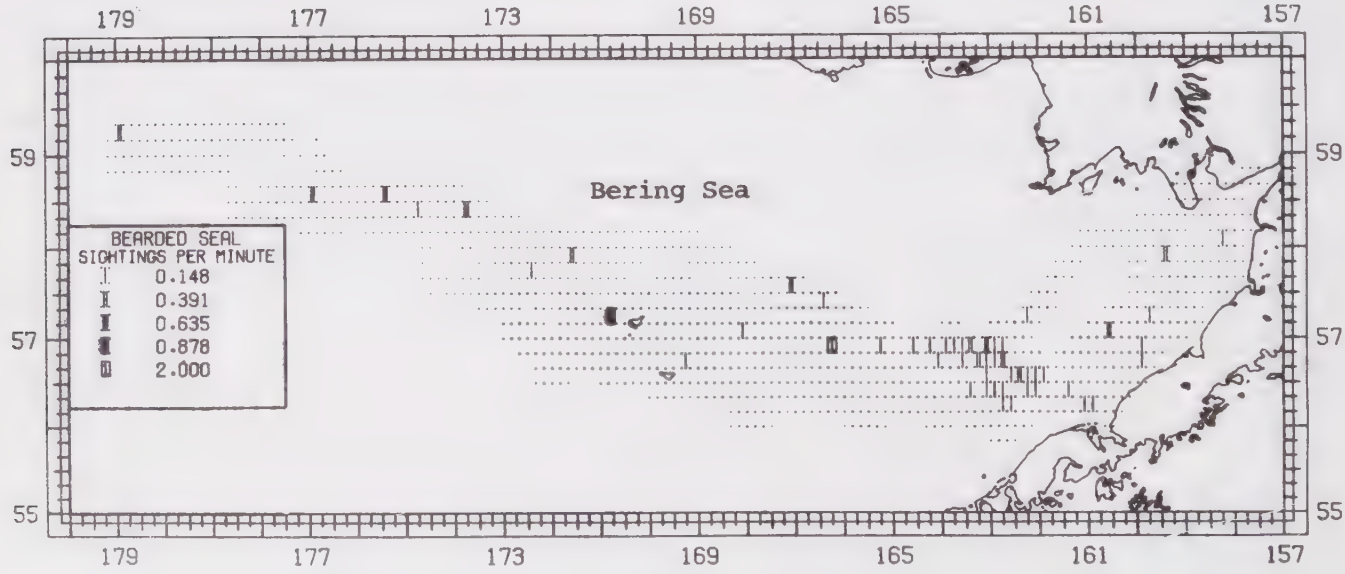


Figure 18.—Computer plot of bearded seal density from ADF&G aerial surveys, 8-23 April 1976.

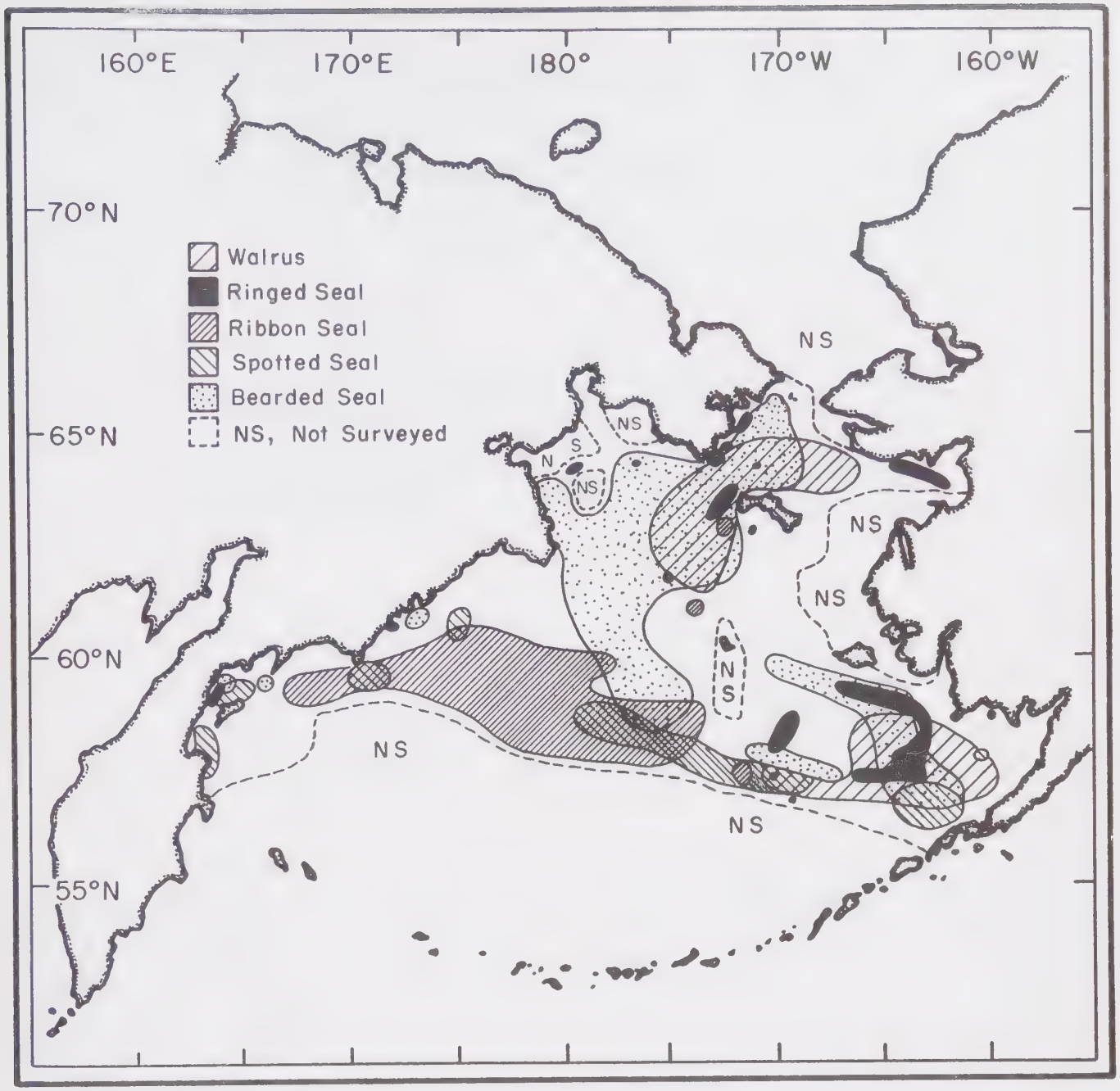


Figure 19.—Centers of abundance of ice-associated pinnipeds in the Bering Sea pack ice, based on numbers sighted per minute during NMFS, ADF&G, and TINRO aerial surveys, 6-26 April 1976. Areas indicated for walrus and spotted seal include only those where at least 2/min were sighted, and for ringed, ribbon, and bearded seal, at least 0.5/min.

Use of Nonmetrical Characters of Skulls of Bering Sea Seals in a Study of the Phenotypic Structure of Their Populations

GENNADII A. FEDOSEEV[1]

ABSTRACT

Analysis of the phenotypic composition of Bering Sea ribbon, *Phoca fasciata*, and spotted, *Phoca largha*, seals shows that these seals differ in degree of differentiation of their populations. The spotted or larga seal shows the greatest differentiation and can be considered as comprising three geographical populations: Karaginskii Gulf, Anadyr Gulf, and eastern Bering Sea. The difference between the Karaginskii and Anadyr groups has been demonstrated previously by their comparative helminth faunas and cranial dimensions. The ribbon seal shows a higher degree of uniformity than does the spotted seal. Ribbon seals residing in the eastern and western Bering Sea are weakly differentiated, indicating a low degree of isolation and high degree of panmixia. In the interest of maintaining stable stocks of these two species, the harvest of each should be evenly distributed among all of its groups.

РЕЗЮМЕ

Анализ фенотипического состава крылатки [*Phoca fasciata*] и ларги [*P. largha*] Берингова моря показал, что эти тюлени имеют разную степень дифференциации их популяций. Ларга по всей вероятности образует три локальные популяции: карагинскую, анадырскую и восточно-беринговоморскую. Различие между карагинской и анадырской ларгой было показано раньше при сравнении их гельминтофауны и размерных признаков черепа. Крылатка имеет большую степень сходства, чем ларга. Слабая морфологическая дифференциация крылатки, обитающей в восточной и западной частях Берингова моря, указывает на низкую степень изоляции и высокую степень панмиксии. В интересах сохранения стабильных запасов этих двух видов, необходимо равномерно распределять добычу между каждыми групповками.

INTRODUCTION

Study of the population as a basic structural unit in the evolution of species occupies a central place in contemporary biology. Knowledge of the phenotypic structure of each populational unit has particular significance in the management of animal populations and their protection, since an understanding of their geographical boundaries, degree of intermixing, mutual relationships, and ecological roles determines to a great extent the approach to solution of fundamental management problems.

The identification of separate populations requires detailed ecological and morphological description of the animals within the boundaries of each geographical region or of the entire species-area. In developing such a description, it is important to bear in mind that one population may not differ from a neighboring one in specific morpho-physiological features that are common to all individuals in it. Instead, they may tend to differ in gene frequency, i.e., in the quantitative expression of various alleles as phenotypes (Yablokov and Yusufov 1976). Genetic analysis of seal populations, as in many other animals, is very difficult. However, a phenotypic approach to the spatial distribution of populations is possible, using discrete elemental features or phenes (Timofeev-Resovskii et al. 1973). The nonmetrical characteristics of the skulls are such features (Berry 1963, 1968).

Definite morphological and ecological differences between seals of the Okhotsk and Bering Seas have been demonstrated previously by Fedoseev (1967),[2] Shustov (1970), and Kosygin and Potelov (1971). Recently, a more detailed study of polymorphism in seals of the Okhotsk Sea was conducted by Fedoseev et al. (1979). In the Bering Sea, morphological differentiation has been demonstrated between the larga or spotted seal, *Phoca largha*, populations of the Karaginskii and Anadyr Gulfs (Gol'tsev et al. 1975[3]).

The present work is a continuation of the studies cited above. In it, I have analyzed the nonmetrical characters of skulls of spotted seals and of ribbon seals, *Phoca fasciata*, from the eastern Bering Sea, east of long. 174°W, and from the central Bering Sea, west of long. 176°W, and in Anadyr Gulf. This was made possible by Soviet-American collaboration in the study of pinnipeds, in which the craniological collections of American and Soviet colleagues were utilized.

METHODS

Skulls of 196 ribbon seals were examined and scored for eight nonmetrical morphological characters (Figs. 1, 2): 1) The locations

[1]Magadan Branch, Pacific Research Institute of Fisheries and Oceanography (MoTINRO), Nagaevskaya 51, Magadan 685013, USSR.

[2]Fedoseev, G. A. 1967. Comparative morpho-ecological characteristics of ringed seals of the Okhotsk Sea and the coastal waters of the Chukchi Peninsula. Avtoreferat Dissertatsii, Magadan.

[3]Gol'tsev, V. N., V. N. Popov, and M. V. Yurakhno. 1975. On the localization of stocks of Bering Sea largas. *In* Marine mammals. Materials 6th all-union conf. 1:100-102. [Abstr.] Naukova Dumka, Kiev.

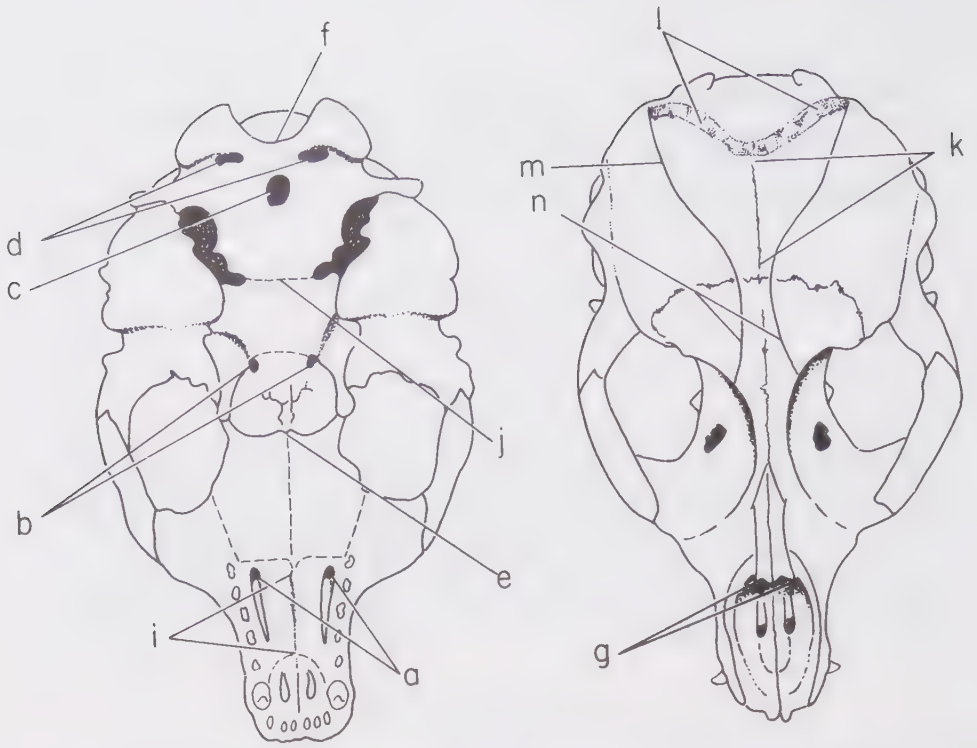


Figure 1.—Nonmetrical characters of seal skulls: a) Position of palatine foramina, b) pterygoid vacuities, c) central vacuity in basioccipital, d) vacuities in condyloid fossae of exoccipitals, e) edge of hard palate, f) ventral border of foramen magnum, g) lateral processes of nasals, i) mid-ventral ridge on intermaxillary suture, j) basioccipital-basisphenoidal suture, k) interparietal suture, l) nuchal crest, m) marginal ridges on temporal fossae, and n) margins of temporal fossae on the frontals.

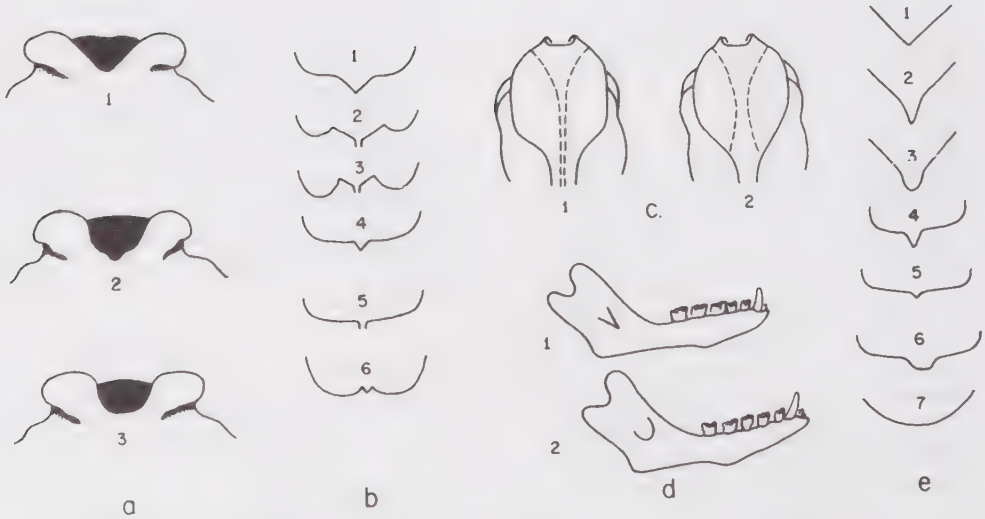


Figure 2.—Variations in form of nonmetrical characters of seal skulls: a) Ventral edge of foramen magnum in ribbon seals, b) posterior edge of hard palate in ribbon seals, c) edges of temporal fossae in spotted seals, d) opening of mandibular foramen, and e) edge of hard palate in spotted seals.

of the palatine foramina relative to the maxillo-palatine suture, 2) the absence or presence and size of the vacuity at the junction of the pterygoid bones with the basisphenoid-presphenoidal suture (i.e., in the area of the pterygoid canal), 3) the absence or presence and size of the mid-ventral vacuity in the pharyngeal tubercle of the basioccipital bone, 4) the absence or presence of the ventro-lateral vacuities in the condyloid fossae of the exoccipital bones, 5) the shape of the posterior edge of the hard palate, 6) the shape of the ventro-anterior edge of the foramen magnum, 7) the relative length of the lateral and medial anterior processes of the nasal bones, and 8) the form of the opening of the mandibular foramen.

Skulls of 123 spotted seals were scored on the basis of 12 characters (Figs. 1, 2): 1) Location of the palatine foramina relative to an imaginary line between the posterior edges of the roots of the fifth post-canine teeth, 2) the absence, presence, and degree of development of the vacuities in the vicinity of the pterygoid canals, 3) absence or presence of the vacuity in the pharyngeal tubercle of the basioccipital bone, 4) absence or presence of the vacuities in the condyloid fossae of the exoccipitals, 5) the shape of the posterior edge of the hard palate, 6) the shape of the opening of the mandibular foramen, 7) the absence and extent when present of the ridge along the mid-ventral suture between the maxillary bones, 8) the condition of the basioccipital-basisphenoidal suture, 9) condition of the interparietal suture, 10) degree of expression of the nuchal crest, 11) degree of expression of the ridges along the medial margins of the temporal fossae, and 12) the convergence or divergence of those margins anteriad, on the frontals. This scheme was modified from a preliminary one kindly provided by A. V. Valetskii and A. V. Yablokov. Some modification of their scheme was required, inasmuch as some of their suggested characters were found to vary with the age of these seals.

The sample proportions (P) of individuals having the character in question (number having character/total number in sample) were compared 1) between sexes within regional samples and 2) within sexes between regional samples. Assuming binomial distribution, the probability of significant differences between the compared samples was determined by estimation of the t-variate, using the formula (Rokitskii 1961):

$$t = \frac{P_1 - P_2}{S_{P_1} + S_{P_2}}$$

where P_1 = the proportion in sample 1
P_2 = the proportion in sample 2
S_{P_1} = the estimated standard error of P_1
S_{P_2} = the estimated standard error of P_2

applying Yates' correction for small samples to P_1 and P_2. The standard error of each sample was estimated as $\sqrt{\frac{P(1-P)}{N}}$.

RESULTS

The comparison of ribbon seals from the central Bering Sea and Anadyr region with those from the eastern Bering Sea on the basis of nonmetrical characters of the skull revealed the following (Table 1).

In the central and Anadyr ribbon seals, significant differences were found between males and females in two characters: 1) The ventrolateral vacuities in the exoccipital bones were absent more often in females than in males (this tendency was reversed in the eastern sample), and 2) the ventral edge of the foramen magnum was more often V-shaped in females than in males (as it tended to be also in the eastern sample).

In the eastern ribbon seals, significant sexual dimorphism was evident in only one character: The central vacuity in the basioccipital bone was more often absent in females than in males (not so in the central sample); when it was present, it tended to be larger in females than in the males (similar tendency in the central sample). Several other dimorphic trends, suggested mutually by the data from both samples, could have been due to chance.

Significant differences among female ribbon seals between the two regions were identified in three nonmetrical characters: 1) The pterygoid vacuities were absent more often in the central than in the eastern sample, 2) the central vacuity in the basioccipital bone was absent more often and tended to be smaller in the central than in the eastern sample (not so in the males), and 3) the shape of the posterior edge of the hard palate was more often notched as in "type 1" in the central than in the eastern sample.

Among the male ribbon seals, the central and eastern samples differed significantly in four characters: 1) The palatine foramina were less often ahead of and more often within the maxillo-palatine suture in the central than in the eastern sample, 2) the shape of the edge of the hard palate was less often of "type 4" and more often of "type 6" in the central sample, 3) the shape of the ventral edge of the foramen magnum tended to be more often of "type 2" in the central animals, and 4) the mandibular foramen was less often rounded and more often acute in the central than in the eastern males.

In the spotted seals from central and eastern Bering Sea, somewhat more sexual dimorphism was evident, and the differentiation between regional samples was expressed much more strongly than in the ribbon seals (Table 2). In the central and Anadyr sample, females differed significantly from males in five characters: 1) The pterygoid vacuities were more often well expressed in females, 2) the exoccipital vacuities were more often absent bilaterally in females, 3) the nuchal crest was more strongly expressed in females than in males, 4) the ridges along the dorsal margins of the temporal fossae were better expressed in males than in females, and 5) those same ridges tended to converge on the frontal bones, forming a crest more often in the males. In the eastern sample, the degree of ridging along the upper edges of the temporal fossae, and the tendency for convergence into a crest on the frontals also tended to differ between sexes, but in both characters the trend was toward greater expression in females than in males.

Both sexes of central spotted seals differed from the eastern sample in having 1) palatine foramina more often ahead of than behind the posterior edges of the 5th postcanines, 2) the central vacuity in the basioccipital bone more irregular in shape, and 3) better expression of ridging on the upper edges of the temporal fossae. The central males (but not the females) also showed 4) more frequent presence of the exoccipital vacuities, and 5) of the central vacuity in the basioccipital bone, as well as 6) a greater tendency for the temporal ridges to form a crest on the frontals, than in the eastern sample.

In the eastern spotted seals, the females showed significantly greater tendency for ridging on the ventral intermaxillary suture, and both sexes showed greater 1) expression of the pterygoid vacuities, 2) opening of the basioccipital-basisphenoidal suture, 3) presence of an interparietal suture, and 4) tendency for the mandibular foramina to be wedge-shaped. In the males (but not in the females), the nuchal crest was better expressed than in the central sample. In most instances, the probability of these differences having been due to chance was $<0.1\%$.

Table 1.—Percentage frequency of occurrence of nonmetrical morphological characters in skulls of ribbon seals of central and eastern Bering Sea, with probability of significant interpopulational differences.

Character	Central area			Eastern area			Probability of difference[1] between central and eastern	
	Females (N=55-59) %f	Males (N=65-69) %f	F:M[1] difference (t)	Females (N=15-17) %f	Males (N=50-51) %f	F:M[1] difference (t)	Females (t)	Males (t)
Location of palatine foramina (Fig. 1a)								
Ahead of maxillo-palatine suture	25.4	24.6	0.12	31.2	47.1	1.02	0.63	2.61*
Behind maxillo-palatine suture	18.6	7.2	1.94	25.0	11.8	1.31	0.73	0.88
Within maxillo-palatine suture	55.9	68.1	1.44	43.8	41.2	0.33	0.58	2.83**
Pterygoid vacuities (Fig. 1b)								
Absent	11.9	11.6	0.74	0.0	5.9	1.14	2.28*	1.07
Large	61.0	68.1	0.85	68.8	70.6	0.30	0.42	0.26
Small	27.1	20.3	0.92	31.2	23.5	0.76	0.49	0.45
Central vacuity in basioccipital (Fig. 1c)								
Absent	20.3	21.7	0.18	0.0	28.0	4.10***	3.48***	0.82
Large	55.9	47.8	0.74	82.4	56.0	2.11*	2.16*	0.70
Small	23.7	30.4	0.84	17.6	16.0	0.33	0.37	1.86
Vacuities in exoccipitals (Fig. 1d)								
Absent	47.3	29.0	2.13*	29.4	43.1	0.90	1.23	1.63
Present, right	52.7	59.4	0.77	58.8	49.0	0.42	0.30	0.95
Present, left	52.7	58.0	0.61	64.7	52.9	0.73	0.74	0.58
Shape, edge of hard palate (Figs. 1e, 2b)								
Type 1	16.9	7.6	1.60	0.0	6.0	1.21	3.03**	0.29
Type 2	3.4	7.6	1.02	0.0	6.0	1.21	0.55	0.29
Type 3	22.0	24.2	0.28	11.8	20.0	0.65	0.85	0.51
Type 4	8.5	6.1	0.53	23.5	24.0	0.12	1.57	2.70**
Type 5	25.4	24.2	0.17	52.9	38.0	0.79	1.77	1.62
Type 6	23.7	28.8	0.64	5.9	6.0	0.28	1.97	3.47***
Shape, ventral edge foramen magnum (Figs. 1f, 2a)								
Type 1	35.1	15.9	2.51*	33.3	29.4	0.46	0.05	1.77
Type 2	22.8	37.7	1.83	20.0	17.6	0.41	0.03	2.51*
Type 3	42.1	46.4	0.47	46.7	52.9	0.13	0.49	0.52
Anterior processes of nasals (Fig. 1g)								
Lateral processes longest	52.7	60.0	0.83	53.3	68.0	1.18	0.12	0.87
Lateral and medial processes equal in length	47.3	40.3	0.79	46.6	32.0	1.17	0.12	0.90
Shape of mandibular foramen (Fig. 2d)								
Rounded	62.7	50.7	1.36	—	70.6	—	—	2.24*
Acute	37.3	49.3	1.36	—	29.4	—	—	2.24*

[1]*P<.05, **P<.01, ***P<.001.

DISCUSSION

Shustov (1970) noted that ribbon seals localize in two main areas in the northern Bering Sea in spring: An eastern area, in the vicinity of St. Matthew, St. Lawrence, and King Islands, and a west-central area in Anadyr Gulf and along the Koryak coast. In his analysis of the dimensions of the body and skull, he found no significant differences between the animals from these two groups. On that basis, he concluded that the eastern and west-central groupings of Bering Sea ribbon seals are not independent, but appear to be panmictic.

The comparison of those groups on the basis of nonmetrical characters reported here indicates that there is some phenotypic and probably weak genetic differentiation of ribbon seals in the eastern and central Bering Sea. Some distinctive differences in the direction of natural selection in the eastern and central areas are to be expected, inasmuch as the living conditions of these seals are not identical in the two areas. The eastern area is shallower and is exposed to the greater warming effect of the Pacific Ocean waters, which results in a unique biocoenosis in that region (Natarov 1963; Moiseev 1964). The central zone is much colder and deeper and supports a distinctly different biocoenosis.

Although there is a tendency toward ecological and genetic differentiation of eastern and central ribbon seals, apparently there is at the same time enough exchange (probably of young animals) between them to minimize their differentiation. Possibility for exchange appears to be greatest in years of less than average ice cover, when the breeding habitat is most restricted. The close similarity of the ribbon seals of the eastern and central Bering Sea indicates that they are not evolutionarily independent but compromise a single geographical population.

In winters with average ice cover, the spotted seal population of the Bering Sea tends to be distributed in three major areas during the breeding season 1) to the southwest, in Karaginskii Gulf, 2) centrally, from Cape Navarin to about long. 176°W, and 3) to the southeast, from the Pribilofs to Bristol Bay. The central group apparently moves northward into Anadyr Gulf in spring. The results of comparisons of samples from the Karaginskii and Anadyr groups have shown great morphological differentiation, as well as differences in the composition of their helminth faunas (Gol'tsev et al. footnote 3). Their differences are great enough to allow consideration of these groups as independent, local populations. The high degree of phenotypic difference between samples of the Anadyr and southeastern Bering Sea groups also indicates great differentiation.

The available information on the ecology of the spotted seal characterizes this as an adaptable species, capable of inhabiting a wide variety of biocoenoses, from oceanic to estuarine. Conversely, the ribbon seal is wholly pelagic in the oceanic environment. The

Table 2.—Percentage frequency of occurrence of nonmetrical morphological characters in skulls of spotted seals of central and eastern Bering Sea, with probability of significant interpopulational differences.

Character	Central area			Eastern area			Probability of difference[1] between central and eastern	
	Females (N=31-36) %f	Males (N=44) %f	F:M[1] difference (t)	Females (N=20-22) %f	Males (N=18-24) %f	F:M[1] difference (t)	Females (t)	Males (t)
Location of palatine foramina (Fig. 1a)								
Ahead of posterior edges 5th postcanines	63.9	70.4	0.38	9.5	8.7	0.12	4.93***	6.45***
Behind posterior edges 5th postcanines	36.1	29.5	0.65	90.5	91.3	0.12	4.94***	6.47***
Ridge along intermaxillary suture (Fig. 1i)								
Present on full length	0.0	2.3	0.89	14.3	4.3	1.17	2.00*	0.63
Present on some part	31.4	47.7	1.47	61.9	69.6	0.55	2.02*	1.52
Absent	68.6	50.0	1.68	23.8	26.1	0.16	3.37**	1.74
Pterygoid vacuities (Fig. 1b)								
Well expressed	34.3	13.6	2.20*	66.7	78.3	0.88	2.19*	6.12***
Weakly expressed	48.6	56.8	0.50	19.0	17.4	0.16	2.38*	3.32**
Absent	17.1	29.5	1.29	14.3	4.4	1.15	0.18	2.97**
Basioccipital-basisphenoidal suture (Fig. 1j)								
Open	0.0	2.3	0.91	9.1	13.0	0.41	1.63	1.59
Partly closed	13.9	13.6	0.07	63.6	69.6	0.43	3.91***	4.84***
Absent	86.1	84.1	0.22	27.3	17.4	0.81	4.96***	6.58***
Vacuities in exoccipitals (Fig. 1d)								
Absent, both sides	22.8	6.8	2.02*	14.3	27.3	1.06	0.72	2.12*
Present, left only	2.8	2.3	0.22	14.3	9.1	0.54	1.53	1.21
Present, right only	5.7	6.8	0.15	9.5	4.5	0.66	0.63	0.20
Present, both sides	68.6	84.1	1.65	61.9	59.1	0.18	0.58	2.21*
Central vacuity in basioccipital (Fig. 1c)								
Absent	14.3	18.2	0.43	31.8	40.9	0.63	1.59	1.99*
Round or oval	25.7	22.7	0.34	50.0	40.9	0.30	1.59	1.58
Irregular form	60.0	56.8	0.26	18.2	18.2	0.00	3.26**	3.17**
Large	57.1	54.5	0.00	18.2	31.8	0.70	3.00**	1.55
Small	28.6	27.3	0.16	50.0	27.3	1.27	1.35	0.00
Interparietal suture (Fig. 1k)								
Present	44.4	45.5	0.08	90.0	100.0	1.54	3.91***	7.27***
Nuchal crest (Fig. 1l)								
Well expressed	41.7	4.5	4.26***	36.4	34.8	0.12	0.34	3.01**
Weakly expressed	58.3	88.6	3.21**	59.1	65.2	0.43	0.01	2.22*
Absent	0.0	6.8	1.72	4.5	0.0	1.04	1.22	1.52
Ridging, margins of temporal fossae (Fig. 1m)								
Well expressed	2.8	31.8	3.81***	0.0	4.4	1.00	0.70	3.24**
Weakly expressed	91.7	63.6	3.24**	63.6	33.3	1.84	2.17*	2.25*
Absent	5.6	4.5	0.31	36.4	62.5	1.53	2.89**	5.28***
Temporal margins on frontals (Figs. 1n, 2c)								
Convergent, forming crest	23.5	47.7	2.28*	25.0	0.0	2.62*	0.21	6.20***
Shape of mandibular foramen (Fig. 2d)								
Rounded, right only	50.0	63.6	1.25	15.0	15.0	0.00	2.70**	4.17***
Rounded, left only	50.0	54.5	0.42	10.0	11.1	0.14	3.38**	3.74***
Wedge-shaped right	50.0	36.4	1.00	85.0	85.0	0.00	2.94**	4.17***
Wedge-shaped left	50.0	45.5	0.18	90.0	88.9	0.14	3.64***	3.74***
Shape, edge of hard palate (Figs. 1e, 2e)								
Type 1	3.2	0.0	1.16	14.3	0.0	1.89	1.44	0.00
Type 2	9.7	0.0	1.91	4.8	0.0	1.05	0.58	0.00
Type 3	0.0	0.0	0.00	4.8	0.0	1.05	1.19	0.00
Type 4	3.2	0.0	1.16	0.0	0.0	0.00	0.77	0.00
Type 5	0.0	0.0	0.00	4.8	4.5	0.06	1.19	1.28
Type 6	64.5	61.4	0.23	42.9	59.0	0.76	1.28	0.28
Type 7	19.4	38.6	1.83	28.6	36.4	0.54	0.82	0.08

[1]*P<.05, **P<.01, ***P<.001.

differentiation of populations of spotted seals probably is favored by their adaptability and, especially, by their social behavior. Whereas the ribbon seal is a solitary animal, seldom congregating in pods under any circumstances, the spotted seal forms very stable family groups during the breeding season and congregates in pods and larger herds immediately thereafter, for the rest of the spring, summer, and autumn. Such pods and herds congregate traditionally at certain estuaries and other feeding areas each year, and they haul out traditionally on certain reefs and islands. Those behaviors suggest the possibility of long-term social and, perhaps, genetic relationships among the members of the pods and even of the herds congregating in traditional sites. As a rule, such relationships between individuals of gregarious species tend to favor genetic differentiation among groups (Haldane 1932; Hinde 1975). The wide dispersal and wholly pelagic existence of the solitary ribbon seal, however, apparently tends to favor panmixia.

CONCLUSION

The ribbon seals in eastern and central Bering Sea are weakly differentiated morphologically, indicating a low degree of isolation

and high degree of mixing. Conversely, the phenotypic analysis of Bering Sea spotted seals has shown quite the reverse: Strong differentiation and apparent semi-isolation of the Karaginskii, Anadyr, and southeastern groups. From the aspect of resource management, the ribbon seals of the Bering Sea appear to be manageable as a single stock, spanning both the Soviet and the American economic zones. The spotted seal population, however, probably should be treated as three stocks: Western, central, and eastern. In the interest of preservation of stable reserves of those three stocks, each probably should be managed separately on the basis of its own distinctive populational and environmental parameters. Each stock inhabits a different biocoenosis, which is affected by a different set of environmental forces. Nevertheless, the harvests should be distributed as evenly as possible among these stocks, in order to maintain their balance and genetic diversity.

ACKNOWLEDGMENTS

The author expresses his sincere acknowledgment and gratitude to A. P. Shustov, V. M. Gol'tsev, G. G. Shmakova, F. H. Fay, J. J. Burns, and A. A. Hoover for their help in this work and for the opportunity of using their craniological collections, as well as to A. V. Yablokov and A. V. Valetskii for their valuable advice in discussing nonmetrical features of the skulls of seals. For their helpful comments on an earlier draft of this paper, the author is grateful to J. J. Burns, F. H. Fay, and B. P. Kelly.

LITERATURE CITED

BERRY, R. J.
1963. Epigenetic polymorphism in wild populations of *Mus musculus*. Genet. Res. 4:193-220.
1968. The biology of non-metrical variation in mice and men. *In* D. R. Brothwell (editor), The skeletal biology of earlier human populations, p. 103-133. Pergamon Press, Lond.

FEDOSEEV, G. A., Yu. A. BUKHTIYAROV, and G. G. SHMAKOVA.
1979. Comparative analysis of craniological characters of the Okhotsk Sea seals with respect to the structure of their populations. Zool. Zh. 58:570-581.

HALDANE, J. B.
1932. The causes of evolution. Longmans, Lond., 235 p.

HINDE, R.
1975. Behavior of animals. Mir, Moscow, 147 p.

KOSYGIN, G. M., and V. A. POTELOV.
1971. Age, sex, and populational variability of craniological characters of the bearded seal. *In* V. A. Arsen'ev and E. A. Tikhomirov (editors), Marine mammals (fur seals and hair seals), p. 266-288. Otdel Nauchno-Tekhnicheskoi Informatsii, Moscow.

MOISEEV, P. A.
1964. Some results of investigations during a Bering Sea scientific harvest expedition. Tr. VNIRO 48:7-29.

NATAROV, V. V.
1963. On the water masses and currents of the Bering Sea. Tr. VNIRO 47:11-133.

ROKITSKII, P. F.
1961. Basic variational statistics for biologists. Belorus. Gos. Univ., Minsk, 329 p.

SHUSTOV, A. P.
1970. Geographic variability of the ribbon seal. Izv. TINRO 70:138-148.

TIMOFEEV-RESOVSKII, N. V., A. V. YABLOKOV, and N. V. GLOTOV.
1973. Outline of the study of populations. Nauka, Moscow, 277 p.

YABLOKOV, A. V., and A. G. YUSUFOV.
1976. Evolutionary science. Vysshaya Shkola, Moscow, 335 p.

New Information on Foods of the Spotted Seal, *Phoca largha*, in the Bering Sea in Spring

YURI A. BUKHTIYAROV,[1] KATHRYN J. FROST,[2] and LLOYD F. LOWRY[2]

ABSTRACT

Information on foods of spotted seals was obtained by analysis of stomach contents from specimens taken in spring in Karaginskii Gulf, Anadyr Gulf, and southeastern, central, and northern Bering Sea. Pollock was the major prey in central Bering Sea and ranked second in Anadyr Gulf. Capelin was the major food in southeastern Bering Sea and ranked second in northern Bering Sea. Arctic cod was the major food in Anadyr Gulf and northern Bering Sea. Sand lance was the major food in Karaginskii Gulf. Most of the fishes eaten were <20 cm in length and <50 g in weight. A comparison of the lengths of Arctic cod eaten by spotted seals and those caught in trawls in northern Bering Sea suggests that the seals may select the larger individuals of that species. Pups ate mostly small crustaceans. Older animals ate mostly fishes, shrimps, and octopus. Maximal quantities of food per stomach ranged from 2.7 to 5.9% of the seal's body weight.

РЕЗЮМЕ

Данные о питании ларги анализировались по содержимому желудков животных, взятых весной в Карагинском, Анадырском заливах и в юго-восточной, центральной и северной частях Берингова моря. Минтай являлся главным источником пищи в центральной части Берингова моря и занимает второе место в Анадырском заливе. Мойва составляла основу питания в юго-восточной части, и занимала второе место в северной части Берингова моря. Сайка преобладала в пище в Анадырском заливе и в северной части Берингова моря. Песчанка была главным источником пищи в Карагинском заливе. Большинство съеденных рыб было меньше 20 см. в длину и весило меньше 50 гр. Сравнение длины сайкы, съеденной ларгой и пойманной тралом в северной части Берингова моря, даёт основание предполагать, что тюлени выбирают более крупную сайку. Ларги-сеголетки питались главным образом мелкими ракообразными. Взрослые животные питались в основном рыбами, креветками и осьминогами. В разных пробах максимальное количество найденной пищи в желудках ларги колебалось от 2,7 до 5,9 процентов веса тела.

INTRODUCTION

The spotted or larga seal, *Phoca largha*, is one of several species of phocine seals which frequent the waters of the Soviet Far East and Alaska. The natural history of this species has been discussed by Burns (1970), Burns et al. (1972), and Shaughnessy and Fay (1977). During February to May, these seals are found in the ice front of the Bering Sea. This is a broad swath of small, dispersed and moving floes in the southern part of the seasonal pack ice, which extends from Alaska to the Siberian coast. Spotted seals give birth, nurse their young, and mate in the ice front. The exact geographical position of the front varies widely between years, but usually is over the continental shelf. As the Bering Sea pack ice begins to break up in May and June, spotted seals concentrate on the remaining ice, where they molt and spend much of their time basking. After the Bering Sea ice has melted, these seals are found near shore, especially in and near estuaries.

The only previous information on the food of spotted seals was from studies in the Okhotsk Sea by Wilke (1954), Fedoseev and Bukhtiyarov (1972)[3], and Nikolaev and Skalkin (1975) and in the Bering Sea by Gol'tsev (1971). The results presented in this paper supplement and extend Gol'tsev's pioneering work.

MATERIALS AND METHODS

We collected information on the foods of spotted seals in March to June. Materials were obtained from seals collected in Karaginskii Gulf and Anadyr Gulf from Soviet research vessels in 1972 and 1973 and from seals collected in southeastern, central, and northern Bering Sea from American research vessels in 1976-78 (Fig.1).

Stomachs and intestines were obtained from seals collected in waters <200 m deep over the continental shelf. Stomachs were slit open longitudinally and the contents removed. In some cases, the contents were examined and analyzed immediately; in others, they were preserved for later analysis. For analysis, the contents were gently sieved on a fine mesh screen and sorted by species. Each component was quantified by weight in Soviet analyses and by volume in American analyses. Weight and volume can be considered identical, since the densities of the prey involved are all close to 1 g/ml. The number of each species (or higher taxon) in each stomach was determined by counts of intact food items or representative hard parts, such as otoliths and other skeletal parts of fishes and beaks of cephalopods. In American studies, otoliths and cephalopod beaks were obtained also from the small intestine, which was slit longitudinally (primarily for parasitological studies) and washed in a pail of water. The contents were allowed to settle and otoliths and beaks were separated from other materials. Counts of otoliths from stomachs and small intestines were combined in

[1]Magadan Branch, Pacific Research Institute of Fisheries and Oceanography (MoTINRO), Nagaevskaya 51, Magadan 685013, USSR.

[2]Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701, USA.

[3]Fedoseev, G. A., and Y. A. Bukhtiyarov. 1972. Food of seals of the Okhotsk Sea. Abstracts 5th all-union conf. stud. marine mammals, 1:110-112. Makhachkala.

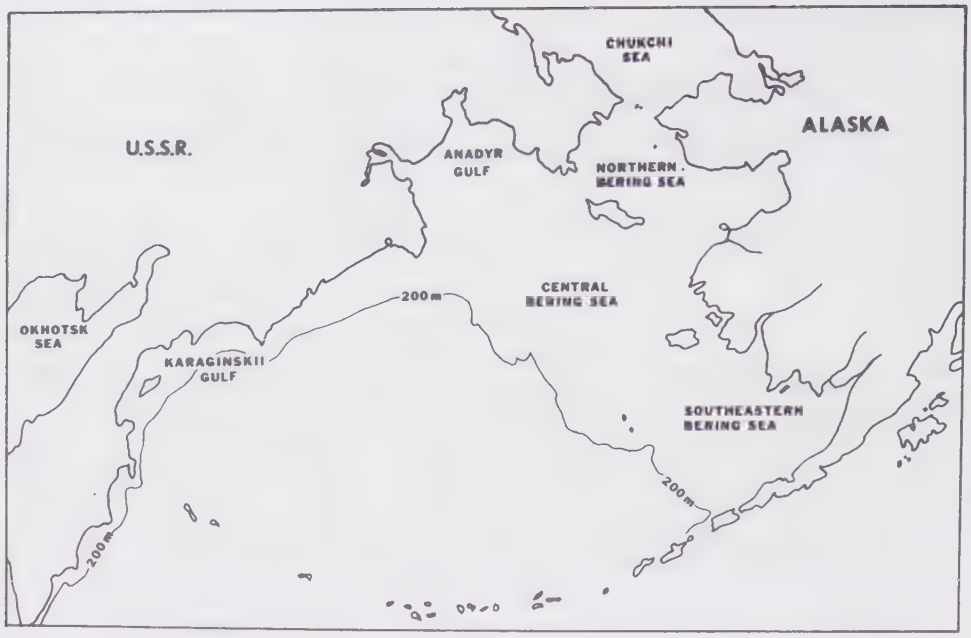


Figure 1.—Map of the Bering Sea showing areas in which spotted seals were collected.

analyses of the data. In some instances the lengths of fresh otoliths were measured to the nearest 0.1 mm with vernier calipers, as indices of size of the fishes.

In areas where seals were collected by American investigators, samples of available prey were collected by means of a 5.8 m headrope, semiballoon otter trawl. The contents of trawl catches were sorted, identified, and weighed. For fishes, the fork length, weight, and the length of the otoliths were measured. Otolith size/fish size relationships were calculated by means of regression analysis (Frost and Lowry 1980, 1981).

Common and scientific names of fishes are from Bailey et al. (1970).

RESULTS

Soviet Studies

Stomachs of over 500 spotted seals were examined, 110 of which contained food remains taken for analysis. Of the samples, 68 were from Karaginskii Gulf and 42 from Anadyr Gulf. A list of the species of prey found in the stomachs is given in Table 1.

In Karaginskii seals, the major food item was sand lance, which comprised 32.4% of the total weight of stomach contents. Other important foods included herring (13.2%) and octopus (10.3%). Unidentifiable fish remains accounted for 14.7%. Nine of the 18 species of prey were shrimps. However, crustaceans in total comprised < 5% of the stomach contents and only *Pandalus hypsinotus* was commonly represented. The largest number of items in a single stomach included 323 sand lance and 9 octopus.

In seals from Anadyr Gulf, fewer species of crustaceans were found, and these did not include large crangonid shrimps. Instead, brachyuran crabs (*Chionoecetes opilio* and *Hyas coarctatus*) and small shrimps of the family Hippolytidae were well represented. As in Karaginskii Gulf, crustaceans comprised < 5% of the total weight of food consumed. Arctic cod (29.5%), pollock (13.6%), and sand lance (9.1%) were the major prey. Remains of octopus occurred in 40% of the stomachs containing food.

Nine of 11 species of prey in stomachs of pups of the year were crustaceans (Table 2). Shrimps of the family Hippolytidae and immature shrimps of the families Pandalidae and Crangonidae were most commonly eaten. Sand lance occurred in approximately one-fourth, and algae occurred in more than one-half, of the stomachs of the seals in this age class.

Fishes and larger shrimps were present in greater quantities than small crustaceans in seals 1 to 4 yr old. Octopus occasionally were present; algae occurred rarely. The average weight of the food mass in this age group was 250 g/stomach with a maximum of 2,300 g.

In sexually mature animals, fishes made up the greatest proportion of the stomach contents. Analysis of the skeletal remains indicated that most of these were large individuals. Crabs as well as shrimps occasionally were present. Octopus occurred more often than in the younger animals.

American Studies

Of 51 seals collected, 31 from the central ($n=5$), southeastern ($n=14$), and northern ($n=12$) Bering Sea contained food remains in the stomach and/or intestine. The species of prey identified are given in Table 1.

Fishes comprised more than 95% of the stomach contents of seals from all areas; octopus comprised 2% in central and 3% in northern Bering Sea. Shrimps were found in only two seals from the northern Bering Sea and amounted to < 1% of the total stomach contents. In central Bering Sea, pollock and eelpout were the major foods; in southeastern Bering Sea, capelin was the major prey, followed by pollock and herring (Table 3). In northern Bering Sea, Arctic cod, capelin, and saffron cod were found most frequently and in the largest numbers.

Four of the spotted seals taken in southeastern Bering Sea were collected from a single locality (lat. 57°40′N, long. 165°01′W) on 20 April 1977. Partially digested remains of 55 capelin and otoliths from two pollock were found in the seal stomachs. In a 20-min tow with an otter trawl at this location, the fishes caught included 28 capelin, 16 pollock, 28 sculpins, and 4 fishes of other species.

Table 1.—Prey taxa identified in spotted seal stomachs in the Bering Sea.

Prey	Karaginskii Gulf	Anadyr Gulf	Northern Bering Sea	Central Bering Sea	Southeastern Bering Sea
Invertebrates					
Neomysis rayi	—	—	X	—	—
Thysanoessa sp.	—	X	—	—	—
Parathemisto libellula	—	—	—	X	—
Pandalus hypsinotus	X	—	—	—	—
Pandalopsis lamelligera	X	—		—	—
Sclerocrangon boreas	X	—	X	—	—
Sclerocrangon salebrosa	X	—	—	—	—
Sclerocrangon intermedia	X	—	—	—	
Argis (=*Nectocrangon*) *lar*	X	—		—	—
Argis (=*Nectocrangon*) *crassa*	X	—	—	—	—
Crangon sp.	X	—	—	—	—
Lebbeus groenlandica	X	X	—	—	—
Eualus gaimardii	—	—	X	—	—
Pagurus sp.	X	X	—	—	—
Chionoecetes opilio	X	X	—	—	—
Hyas coarctatus	—	X	—	—	—
Bivalve mollusk	X	—	—	—	—
Octopus sp.	X	X	X	X	—
Fishes					
Clupea harengus (Pacific herring)	X	X	X	—	X
Mallotus villosus (capelin)	—	—	X	—	X
Boreogadus saida (Arctic cod)	X	X	X	—	X
Eleginus gracilis (saffron cod)	X	X	X	—	X
Theragra chalcogramma (walleye pollock)	—	X	X	X	X
Lycodes sp. (eelpout)	—	—	X	X	—
Lumpenus sp. (prickleback)	—	—	—	X	—
Ammodytes hexapterus (Pacific sand lance)	X	X	X	—	—
Hexagrammos sp. (greenling)	—	X	—	—	—
Family Cottidae (sculpins)	—	X	—	—	—
Gymnocanthus sp.	—	—	X	—	—
Icelus sp.	—	—	—	X	—
Myoxocephalus sp.	—	—	X	—	X
Triglops sp.	—	—	—	—	X
Family Pleuronectidae (flatfish)	—	X	X	—	X
Algae	X	X	—	—	—

Most of the fishes eaten by spotted seals in northern Bering Sea were < 20 cm in length and < 50 g in weight (Table 4). Larger fishes, particularly large sculpins, are sometimes eaten, but in such cases, the head of the fish may not be eaten.[4] Therefore, the otoliths of such fishes would not be present in the stomach or intestine. In our studies we did not find skeletal remains of fishes larger than those shown in Table 4.

The fresh condition of the stomach contents in 13 of the seals collected in southeastern Bering Sea indicated that they were actively feeding at the time of collection. In these, volumes of stomach contents ranged from 45 ml in a seal that had eaten capelin to 1,535 ml in a seal that had eaten herring. The mean volume of stomach contents in these seals was 491.5 ml, amounting to about 0.9% of the total body weight of the seals (range 0.08 to 2.7%).

The range in size of Arctic cod caught by the otter trawl compared with those caught by the seals was very similar (Fig. 2). The cod eaten by the seals, however, tended to be slightly longer ($\bar{x}$=14.9 cm, n=326) than those caught in the trawls ($\bar{x}$=14.2 cm, n=121). Of the Arctic cod caught in the trawls, 38/121 (31.4%) were < 12 cm long, while only 33/326 (13.5%) of those eaten by the seals were < 12 cm long. These differences in proportions are highly significant (χ^2=21.353, P< 0.01) and indicate that the 1-yr-old Arctic cod (7-12 cm long), which were strongly represented in the trawl catches, were not commonly eaten by the seals.

DISCUSSION

At least 18 species of invertebrates and 15 species of fishes were identified from the stomach and intestinal contents of spotted seals collected in the Bering Sea in spring. Sixteen of the invertebrate species were crustaceans, 10 of which were shrimps. The number of prey species identified from seals collected in central and southeast-

[4]J. J. Burns, Game Biologist IV, Alaska Department of Fish and Game, Fairbanks, AK 99701, pers. commun. June 1979.

Table 2.—Percentage frequency of occurrence of prey taxa in stomachs of spotted seals in relation to age class.

Prey	Age class of seals		
	Pups $n=27$	1 to 4 yr $n=21$	5 or more yr $n=35$
Thysanoessa sp.	—	—	2.8
Decapod crustaceans	—	4.8	—
Pandalus hypsinotus	7.4	4.8	5.7
Pandalus sp.	3.7	14.2	14.2
Pandalopsis lamelligera	—	4.8	—
Sclerocrangon boreas	—	—	2.8
Sclerocrangon salebrosa	—	—	2.8
Sclerocrangon intermedia	3.7	—	—
Sclerocrangon sp.	3.7	—	2.8
Argis (=*Nectocrangon*) *lar*	—	4.8	—
Argis (=*Nectocrangon*) *crassa*	3.7	—	—
Crangon sp.	3.7	—	—
Family Hippolytidae	7.4	—	—
Lebbeus groenlandica	—	4.8	—
Pagurus sp.	3.7	—	—
Chionoecetes opilio	3.7	—	8.5
Hyas coarctatus	—	—	2.8
Bivalve mollusks	—	4.8	2.8
Octopus sp.	—	9.5	31.4
Unidentified fishes	—	14.2	25.7
Clupea harengus	—	9.5	14.2
Ammodytes hexapterus	25.9	38.0	25.7
Eleginus gracilis	—	—	2.8
Boreogadus saida	—	4.8	11.4
Theragra chalcogramma	—	—	2.8
Family Cottidae	—	—	2.8
Family Pleuronectidae	—	4.8	—
Hexagrammos sp.	—	—	2.8
Algae	51.8	4.8	—

ern Bering Sea was less than in other areas. The largest number of prey species was identified in samples from Karaginskii Gulf. In general, the number of species identified was positively correlated with sample size. In northern Bering Sea, however, 14 prey species were found in 12 seals examined, while in southeastern Bering Sea only 8 prey species were found in 14 seals.

In spring in the Bering Sea, fishes, shrimps, and octopus comprised most of the food of spotted seals in all areas, but the principal species eaten differed among areas. Pollock was the major food in central Bering Sea and ranked second in Anadyr Gulf. Pollock have been reported to be the main prey of these seals in the Okhotsk Sea (Wilke 1954; Fedoseev and Bukhtiyarov footnote 3). Capelin was the primary food in southeastern Bering Sea and ranked second in northern Bering Sea. Arctic cod was the major prey in Anadyr Gulf and northern Bering Sea. Sand lance was the major food in

Table 4.—Size characteristics of fishes eaten by spotted seals in northern Bering Sea.

Prey	No. otoliths measured	Size of fishes estimated from otolith length			
		Length (cm)		Weight (g)	
		Mean	Range	Mean	Range
Boreogadus saida	326	14.9	7.6-20.5	24.9	2.2- 73.9
Eleginus gracilis	131	16.7	6.2-25.1	36.4	1.4-144.6
Theragra chalcogramma	21	10.9	8.0-15.0	8.4	3.3- 20.0
Lycodes sp.[1]	6	27.3	22.3-30.9	73.4	38.0-103.1
Family Cottidae[2]	19	10.0	3.3-16.5	14.5	0.3- 44.1
Mallotus villosus[3]	—	—	9.0-14.2	10.1	4.5- 16.1
Clupea harengus[3]	—	—	8.6-27.2	12.5	5.0-180.0
Ammodytes hexapterus[3]	—	—	6.6-11.9	2.3	0.5- 4.5

[1]Based on otolith length to fish length and weight relationships for *Lycodes palearis*.

[2]Based on otolith length to fish length and weight relationships for *Myoxocephalus* sp.

[3]Based on sizes of fishes caught by otter trawl in the area in which seals were collected.

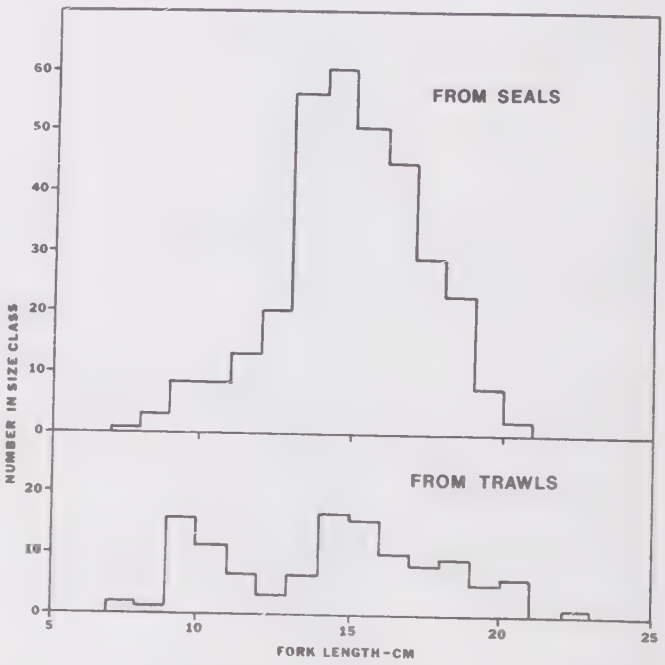


Figure 2.—Length-frequency distribution of Arctic cod, *Boreogadus saida*, obtained from trawl samples and from stomachs of spotted seals in the same areas of northern Bering Sea. Fork lengths of fishes from seal stomachs were estimated from otolith lengths.

Table 3.—Fishes identified from otoliths in stomachs and intestines of spotted seals taken in the Bering Sea.

Species	Central Bering ($n=5$)		Southeastern Bering ($n=14$)		Northern Bering ($n=12$)	
	Total number of fishes (%)	Frequency of occurrence (%)	Total number of fishes (%)	Frequency of occurrence (%)	Total number of fishes (%)	Frequency of occurrence (%)
Theragra chalcogramma	88	80	5	43	2	8
Boreogadus saida	—	—	1	7	51	92
Eleginus gracilis	—	—	1	7	15	42
Clupea harengus	—	—	5	14	4	25
Mallotus villosus	—	—	89	86	19	42
Ammodytes hexapterus	—	—	—	—	4	25
Lycodes spp.	11	80	—	—	1	8
Lumpenus sp.	1	20	—	—	—	—
Family Cottidae	1	20	1	21	5	42
Family Pleuronectidae	—	—	1	7	1	25

[1]Less than 1%.

Karaginskii Gulf. Herring was of minor importance in all areas. Herring and rainbow smelt, *Osmerus mordax*, are major foods of spotted seals in southeastern Chukchi Sea in early summer and autumn (Frost and Lowry unpubl. data), as well as along southwestern Seward Peninsula in autumn (J. J. Burns footnote 4). In general, the regional and seasonal differences in foods of spotted seals appear to be related to the seasonal distribution and abundance of the principal species of forage fishes.

The comparison of seal stomach and otter trawl contents from southeastern Bering Sea suggests that selection of prey does occur. Capelin comprised 36.8% of the number of fishes caught in the trawl, while pollock and sculpins accounted for 21.0 and 36.8%, respectively. Since no pollock or sculpin bones were found in the stomachs, we concluded that the seals were feeding selectively on capelin when collected. Spotted seals sometimes eat pollock and sculpins in appreciable quantities (Table 3), but in this instance they apparently had selected for capelin or against pollock and sculpins.

Most of the fishes eaten by these seals are swallowed whole. The results in Figure 2 indicate that, given access to fishes of different sizes, the seals selected certain size classes, possibly those most easily caught and swallowed.

The quantity of food found in each stomach usually was small, relative to the weight of the seals. The maximal quantity from Soviet samples was about 4.1% of the average body weight and from the American samples, only 2.7%. Gol'tsev (1971) reported a maximum of 3,300 g, which would be about 5.9% of the body weight of a medium-sized seal. Keyes (1968) reported that phocid seals in captivity eat 6-10% of their body weight per day. Ashwell-Erickson et al. (1979) reported that the food intake of two captive spotted seals declined from 13% of the body weight per day during the first year of life to 3% at age 9 yr. The quantity of food in the stomach of a seal at any given time varies widely and does not appear to be directly related to the daily food requirement. More information is needed on the rate of food consumption, amount of time spent feeding, and rate of food passage through the stomach.

The differences found in this study between age classes in kinds of prey consumed were similar to those reported by Gol'tsev (1971) and Popov and Bukhtiyarov (1975)[5]. Spotted seals in their first year of life tend to eat mostly small crustaceans (amphipods, shrimps, and euphausiids) and commonly eat algae, sticks, and other debris. These kinds of items were not found in older animals. Animals 1 to 4 yr old mostly ate fishes, larger shrimps, and occasionally octopus. Those 5 yr or older fed more on benthic organisms, such as crabs and octopus. Similar changes in diet with age have been observed in ringed seals, *Phoca hispida*, in northern Bering and Chukchi Seas (Lowry et al. 1980).

Most of the prey species eaten by spotted seals in the Bering Sea also are eaten by other marine mammals and by seabirds and fishes (McAlister and Perez 1976)[6]. Many of the same species also are harvested in commercial fisheries (Lowry et al. 1979). A detailed understanding of the trophic interrelationships of major marine consumers in this area is essential for the design of national policies for marine resource utilization and conservation. Further studies of the foods of spotted seals and other Bering Sea pinnipeds by both Soviet and American scientists are needed to supply the information required for multispecies resource management.

[5]Popov, V. N., and Y. A. Bukhtiyarov. 1975. On age-related changes in feeding and helminth faunas of spotted seals in the Okhotsk Sea. Abstracts 6th all-union conf. marine mammals, 2:62-64. Naukova Dumka, Kiev.

[6]McAlister, W. B., and M. A. Perez. 1976. Ecosystem dynamics: Birds and marine mammals. Part I. Preliminary estimate of pinniped-finfish relationships in the Bering Sea. Final report R.U. 77, 29 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

ACKNOWLEDGMENTS

We thank the officers and crews of the ships from which this research was conducted for their encouragement and support. American studies were funded in part by the Bureau of Land Management through interagency agreement with the National Oceanic and Atmospheric Administration, as part of the Outer Continental Shelf Environmental Assessment Program and in part by Federal Aid in Wildlife Restoration Project W-17-9. Francis H. Fay, Clifford H. Fiscus, Ole A. Mathisen, Kenneth W. Pitcher, and Victor B. Scheffer reviewed the manuscript and offered helpful comments. Kathy Valentine typed and edited the manuscript.

LITERATURE CITED

ASHWELL-ERICKSON, S., R. ELSNER, and D. WARTZOK.
1979. Metabolism and nutrition of Bering Sea harbor and spotted seals. Proc. Alaska Sci. Conf. 29:651-665.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, and W. B. SCOTT.
1970. A list of common and scientific names of fishes from the United States and Canada. 3rd ed. Am. Fish. Soc. Spec. Publ. 6, 150 p.

BURNS, J. J.
1970. Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi Seas. J. Mammal. 51:445-454.

BURNS, J. J., G. C. RAY, F. H. FAY, and P. D. SHAUGHNESSY.
1972. Adoption of a strange pup by the ice-inhabiting harbor seal, *Phoca vitulina largha*. J. Mammal. 53:594-598.

FROST, K. J., and L. F. LOWRY.
1980. Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. Can. J. Zool. 58:1601-1607.
1981. Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships. Fish. Bull., U.S. 79:187-192.

GOL'TSEV, V. N.
1971. Feeding of the harbor seal. Ékologiya 2:62-70.

KEYES, M. C.
1968. The nutrition of pinnipeds. *In* R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice, and R. J. Schusterman (editors), The behavior and physiology of pinnipeds, p. 359-395. Appleton-Century-Crofts, N.Y.

LOWRY, L. F., K. J. FROST, and J. J. BURNS.
1979. Potential resource competition in the southeastern Bering Sea: fisheries and phocid seals. Proc. Alaska Sci. Conf. 29:287-296.
1980. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. Can. J. Fish. Aquat. Sci. 37:2254-2261.

NIKOLAEV, A. M., and V. A. SKALKIN.
1975. On the food of true seals of the eastern coast of Sakhalin. Izv. TINRO 95:120-125.

SHAUGHNESSY, P. D., and F. H. FAY.
1977. A review of the taxonomy and nomenclature of North Pacific harbour seals. J. Zool. (Lond.) 182:385-419.

WILKE, F.
1954. Seals of northern Hokkaido. J. Mammal. 35:218-224.

Helminthological Comparison of Subpopulations of Bering Sea Spotted Seals, *Phoca largha* Pallas

SEMYON L. DELYAMURE,[1] MIKHAIL V. YURAKHNO,[1] VALENTIN N. POPOV,[1]
LARRY M. SHULTS,[2] and FRANCIS H. FAY[2]

ABSTRACT

The population of spotted seals in the Bering Sea appears to consist of three major groups, which concentrate at the time of giving birth and mating in Karaginskii Gulf, the Navarin-Anadyr region, and in southeastern Bering Sea from the Pribilof Islands to Bristol Bay, respectively. As part of an investigation of the biological characteristics of the seals in each group, their helminth faunas were compared. Samples consisted of 122 seals from the Karaginskii region, 130 from the Navarin-Anadyr region, and 57 from the Pribilof-Bristol Bay region. Of 22 species of helminths isolated from these seals, only 10 were common to all three regional samples, and most differed to a significant degree among regions in both prevalence and intensity of infection. The seals of the Karaginskii and Pribilof regions had fewer species of helminths in common (11) than either had with the Anadyr group (13), but were significantly more similar in the prevalences of the respective helminths. In numbers of helminths per host, the Anadyr and Pribilof seals were much more similar than either was to the Karaginskii seals. The differences between regional samples appear to be attributable in part to the somewhat different assemblages of prey available and, perhaps in part, to regional food preferences derived from learned, traditional, or inherited behaviors.

РЕЗЮМЕ

Популяция ларги в Беринговом море по-видимому состоит из трех главных групп, которые сосредоточиваются во время рождения и спаривания в Карагинском заливе, в Наварин-Анадырском районе, и в юго-восточной части Берингова моря от Прибыловских островов до Бристольского залива. В связи с исследованием биологических особенностей этих тюленей в каждой группе сравнивалась их гельминтофауна. Пробы получены от 122 ларг из Карагинского залива, 130 из Анадырского залива, и 57 из Прибылово-Бристольского района. Только 10 из 22 видов гельминтов являются общими для всех трёх районов; однако степень интенсивности и экстенсивности инвазии значительно изменяется в каждом из этих районов. Карагинская и Прибыловская популяции имели 11 общих видов гельминтов, но каждая из этих популяций имела 13 видов гельминтов общих с анадырской группой. Анадырские и прибыловские тюлени наиболее сходные по интенсивности инвазии. Разница между региональными пробами отчасти может быть обусловлена локальными особенностями питания, а с другой стороны - рационом, определяемым приобретенным, традиционным или унаследованным поведением тюленей.

INTRODUCTION

Spotted or larga seals, *Phoca largha*, inhabit the seas bounding the northern part of the Pacific Ocean, wherever pack ice is a dominant physical feature in winter (Mohr 1965; Chapskii 1969; Shaughnessy and Fay 1977). During their breeding season in early spring, the spotted seals of the Bering Sea are associated with the southern part of the pack ice, within about 100 km of its edge. Surveys of their distribution in April to early May, at the time of parturition and mating, repeatedly have disclosed a consistent pattern of varying abundance in different sectors of the ice (Tikhomirov and Kosygin 1966; Gol'tsev et al. 1975,[3] 1978; Burns and Harbo 1977[4]). The seals tend to concentrate at that time principally in three regions: 1) In Karaginskii Gulf, 2) south of Cape Navarin to St. Matthew Island, and 3) in southeastern Bering Sea, from the Pribilof Islands to outer Bristol Bay (Braham et al. 1984). Later in the spring, with melting and recession of the pack ice, the Karaginskii seals apparently disperse to Kamchatkan and Koryak nearshore waters, the Navarin-St. Matthew seals move northward into Anadyr Gulf, while the others continue through the Bering Strait, into the Chukchi Sea. They summer principally in coastal and estuarine habitats.

Because the three concentrations appear to be semi-isolated during the breeding season, they may warrant separate consideration in the formulation of management procedures. In order to assess the degree of their isolation, series of specimens have been collected from each group in recent years, for comparison of their craniological and helminthological characteristics. The results of the helminthological investigations are presented in this report.

MATERIALS AND METHODS

Helminthological data from the Karaginskii Gulf breeding concentration were obtained from 122 seals taken there between 6 and

[1]Laboratory of Marine Mammal Parasitology, Frunze State University, Simferopol' 333036, USSR.

[2]Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, USA.

[3]Gol'tsev, V. N., V. N. Popov, and M. V. Yurakhno. 1975. On the localization of stocks of Bering Sea largas. *In* Marine mammals. Materials 6th all-union conf. 1:100-102. [Abstr.] Naukova Dumka, Kiev.

[4]Burns, J. J., and S. J. Harbo, Jr. 1977. An aerial census of spotted seal, *Phoca vitulina largha*, and walruses, *Odobenus rosmarus*, in the ice front of Bering Sea. *In* Environmental assessment of the Alaskan continental shelf. Quarterly reports of principal investigators, April-June 1977, Vol. 1, p. 58-132. NOAA Environ. Res. Lab., Boulder, Colo.

28 May 1972 (examined by Popov). In the Navarin-Anadyr concentration, data were obtained from 116 seals taken in Anadyr Gulf between 8 April and 16 June 1967 (Yurakhno), and from 14 taken there between 5 May and 11 July 1972 (Popov). Data for the Pribilof-Bristol Bay concentration were obtained from 26 seals taken in the vicinity of the Pribilof Islands between 17 and 28 April 1976 (Yurakhno), 15 in southern Bristol Bay between 25 March and 25 April 1976 (Shults); 8 about 275 km north of the Pribilof Islands between 22 March and 26 April 1977 (Shults); and 8 about 450 km north of the Pribilofs between 26 May and 4 June 1977 (Shults). The geographic position of each sample is shown in Figure 1.

For each seal, the contents of the heart, lungs, gall bladder, stomach, and both the large and the small intestines were examined thoroughly. All helminths from them were then washed in fresh- or seawater and fixed in 10% Formalin.[5] Later, in the laboratory, they were examined and identified by conventional methods.

The resultant data were treated statistically, following Beklemishev (1970) and Breev (1976), by Student's t-test for significance of difference between sample means:

$$t = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{S_1^2 + S_2^2}}$$

where $\bar{x}$ = sample mean, assuming binomial distribution
S = standard deviation about the sample mean.

When the value of t was > 2.0, the differences between regional samples were considered to be significant at the 0.95 level; when $t >$ 3.03, the difference was accepted as significant at the 0.999 level.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

The qualitative and quantitative characteristics of the helminths from spotted seals in the samples from the three compared concentrations are presented in Tables 1 to 3 and in Figures 2 and 3.

The results of comparison of the helminth faunas of the Karaginskii and Anadyr populations already have been published (Gol'tsev et al. 1978). Therefore, we confine ourselves here principally to comparison of the helminths of the southeastern Bering Sea seals with those from the Anadyr and Karaginskii regions. Larval forms of helminths were excluded from the comparison.

From Table 1, one can see that the species composition of the helminths in the seals from each of the three regions was similar; nevertheless, only 10 of the 22 species were shared. These included several widely prevalent parasites of marine mammals (Delyamure et al. 1979): The trematode *Phocitrema fusiforme*; the cestode *Anophryocephalus* sp.;[6] the acanthocephalans *Corynosoma semerme, C. strumosum, C. validum*, and *C. villosum*; and the nematodes *Anasakis simplex, Phocascaris cystophorae, Terranova* sp. (footnote 6), and *Dipetalonema spirocauda*.

The qualitative similarity of the helminth fauna of the seals from southeastern Bering Sea to those in the Karaginskii and Navarin-Anadyr regions lay almost exclusively within those 10 species. The only other resemblances were 1) to the Karaginskii seals in the presence of the cestode *Diplogonoporus tetrapterus*, and 2) to the Navarin-Anadyr seals in the presence of the trematode *Orthosplanchnus arcticus*, the cestode *Diphyllobothrium* sp., and the nematode *Contracaecum osculatum*. The remaining species did not occur in common.

[6]The authors are not in full agreement as to the specific identification of cestodes of the genus *Anophryocephalus*, nematodes of the genus *Terranova* (=*Phocanema*), and acanthocephalans of the genus *Bolbosoma*, hence these are indicated here as indeterminate species ("sp."), pending further study.

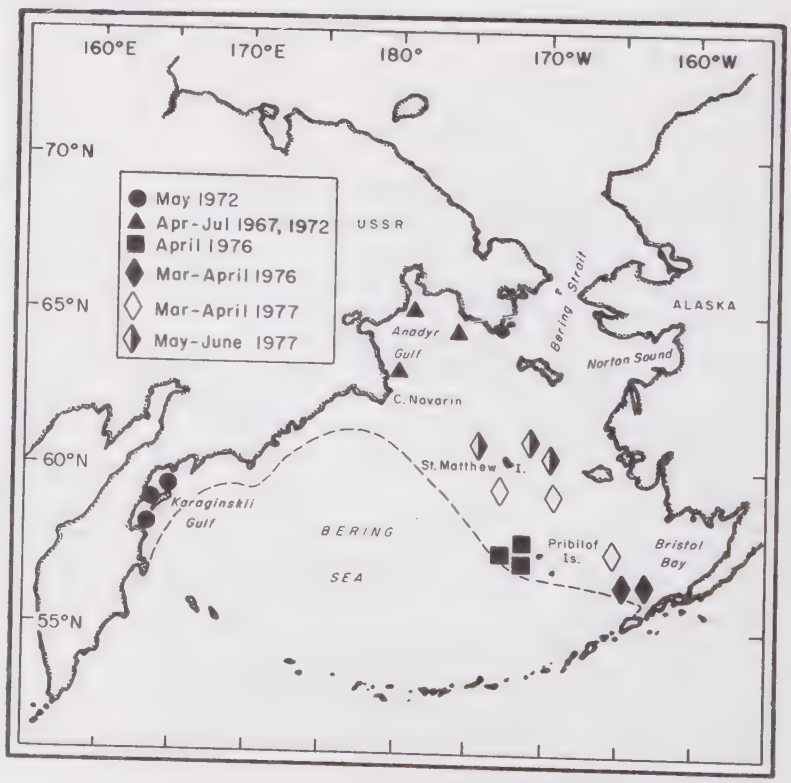


Figure 1.—Locations in which samples of spotted seals were taken for helminthological investigation in the Bering Sea. Dashed line marks approximate maximal extent of winter pack ice.

Table 1.—Comparative percentage frequency of occurrence of species of helminths in spotted seals taken in Karaginskii and Anadyr Gulfs and in the Pribilof-Bristol Bay region of Bering Sea.

Species of helminth	1 Karaginskii (n=122) $\bar{x} \pm S$	2 Anadyr (n=130) $\bar{x} \pm S$	3 Pribilof (n=57) $\bar{x} \pm S$	t_{1-2}	t_{1-3}	t_{2-3}
Orthosplanchnus arcticus	—	8.5±2.43	1.8±1.73	—	—	2.25
Orthosplanchnus pygmaeus	0.8±0.81	—			—	
Phocitrema fusiforme	29.5±4.11	10.8±2.72	1.8±1.73	3.78	6.22	2.81
Microphallus orientalis	—	—	1.8±1.73	—	—	—
Anophryocephalus sp.[1]	24.5±3.76	23.8±3.74	56.1±6.56	0.13	4.18	4.28
Diphyllobothrium sp.	—	2.3±1.32	7.0±3.38	—	—	1.29
Diplogonoporus tetrapterus	1.7±1.15	—	8.8±3.78	—	1.80	—
Pyramicocephalus phocarum	—	—	1.8±1.73	—	—	—
Diphyllobothriidae gen. sp.	3.3±1.61	—	1.8±1.73	—	0.05	—
Corynosoma semerme	45.8±4.51	54.6±4.36	[2]88.1±4.99	1.40	6.30	5.07
Corynosoma strumosum	87.0±3.05	81.6±3.39	93.0±3.38	1.19	1.32	2.39
Corynosoma validum	8.2±2.48	4.6±1.18	3.5±2.44	1.31	1.35	0.40
Corynosoma villosum	2.5±1.40	3.0±1.50	3.5±2.44	0.28	0.37	0.16
Corynosoma wegeneri	6.2±2.24	8.5±2.43	—	0.58	—	—
Bolbosoma sp.[1]	—	—	5.3±2.96	—	—	—
Anisakis simplex	36.1±4.35	2.3±1.32	7.0±3.38	7.44	5.29	1.31
Contracaecum osculatum	—	2.3±1.32	31.6±6.30	—	—	4.54
Phocascaris cystophorae	54.9±4.50	72.3±3.93	52.6±6.60	2.92	0.29	2.57
Terranova sp.[1]	65.3±4.31	33.1±4.12	50.9±6.61	5.40	1.82	2.29
Terranova decipiens[1]	1.6±1.15	4.6±1.84	—	1.37	—	—
Anisakidae gen. sp.	—	0.8±0.77	—	—	—	—
Otostrongylus circumlitus	—	—	1.8±1.73	—	—	—
Parafilaroides krascheninnikovi	2.4±1.38	0.8±0.77	—	1.04	—	—
Dipetalonema spirocauda	4.0±1.77	8.5±2.44	1.8±1.73	1.47	0.92	3.41

[1]Species in question; authors disagree on identifications.
[2]Based on sample size of 42 seals.

Table 2.—Comparative abundance (number per host) of each species of helminth in spotted seals taken in Karaginskii and Anadyr Gulfs and in the Pribilof region[1] of Bering Sea.

Species of helminth	1 Karaginskii (n=122) $\bar{x} \pm S$	2 Anadyr (n=130) $\bar{x} \pm S$	3 Pribilof (n=26) $\bar{x} \pm S$	t_{1-2}	t_{1-3}	t_{2-3}
Orthosplanchnus arcticus	—	1.5± 0.97	0.3± 0.26	—	—	1.25
Orthosplanchnus pygmaeus	0.0± 0.01	—	—	—	—	—
Phocitrema fusiforme	p[2]	p	p	—	—	—
Microphallus orientalis	—	—	p	—	—	—
Anophryocephalus skrjabini[3]	10.2± 3.47	p	1.7± 0.81	—	2.38	—
Diphyllobothrium sp.	—	0.0± 0.05	p	—	—	—
Diplogonoporus tetrapterus	0.1± 0.06	—	1.9± 1.84	—	0.99	—
Pyramicocephalus phocarum	—	—	0.2± 0.15	—	—	—
Diphyllobothriidae gen. sp.	0.1± 0.10	—	0.1± 0.08	—	0.08	—
Corynosoma semerme	2.7± 0.48	14.4± 3.26	8.5± 1.43	2.71	3.85	1.65
Corynosoma strumosum	119.0±87.60	835.0±208.00	397.0±103.00	3.18	2.04	1.89
Corynosoma validum	0.2± 0.08	0.1± 0.08	0.1± 0.08	1.10	0.83	0.28
Corynosoma villosum	0.1± 0.06	0.0± 0.02	0.2± 0.09	0.67	0.73	1.44
Corynosoma wegeneri	0.3± 0.24	0.6± 0.30	—	0.76	—	—
Bolbosoma nipponicum[3]	—	—	p	—	—	—
Anisakis simplex	11.9± 1.13	0.1± 0.10	0.4± 0.14	10.4	10.1	1.45
Contracaecum osculatum	—	0.1± 0.06	p	—	—	—
Phocascaris cystophorae	7.0± 0.62	16.9± 3.03	7.7± 1.32	3.18	0.47	2.79
Terranova azarasi[3]	13.0± 2.31	4.3± 1.10	3.4± 1.02	3.14	3.80	0.56
Terranova decipiens[3]	0.2± 0.19	0.6± 0.53	—	0.71	—	—
Anisakidae gen. sp.	—	0.0± 0.01	—	—	—	—
Otostrongylus circumlitus	—	—	0.3± 0.31	—	—	—
Parafilaroides krascheninnikovi	0.1± 0.10	0.0± 0.02	—	0.99	—	—
Dipetalonema spirocauda	0.8± 0.69	0.8± 0.63	p	0.05	—	—

[1]Includes only the April 1976 (Yurakhno) sample; comparable data not available from others.
[2]Present but not counted.
[3]Species in question; authors disagree on identifications.

Table 3.—Comparative diversity of species of helminths in spotted seals of different ages, taken in Karaginskii and Anadyr Gulfs and in the Pribilof region[1] of Bering Sea.

Age of seals	1 Karaginskii			2 Anadyr			3 Pribilof					
	n	$\bar{x} \pm S$	C.V.[2]	n	$\bar{x} \pm S$	C.V.	n	$\bar{x} \pm S$	C.V.	t_{1-2}	t_{1-3}	t_{2-3}
Newborn	8	—	—	7	—	—	2	—	—	—	—	—
Yearlings	18	1.4±0.27	102.0	18	0.4±0.26	286.0	—	—	—	2.66	—	—
1-4 yr	46	4.5±0.23	34.5	45	3.8±0.18	31.6	5	3.8±0.16	9.5	2.28	2.36	0.00
5-12 yr	27	4.4±0.38	23.2	44	4.3±0.20	31.4	12	4.4±0.28	21.5	0.40	0.04	0.44
13 yr and older	23	4.6±0.21	23.6	14	4.1±0.46	41.8	7	4.7±0.28	20.6	0.92	0.27	1.06
Age unknown	—	—	—	2	3.5±0.35	14.3	—	—	—	—	—	—
Total	122	3.7±0.18	52.1	130	3.3±0.17	59.0	26	4.0±0.28	35.9	1.71	0.90	2.19

[1]Includes only the April 1976 (Yurakhno) sample; comparable data not available from others.
[2]C.V. = coefficient of variation about the sample mean.

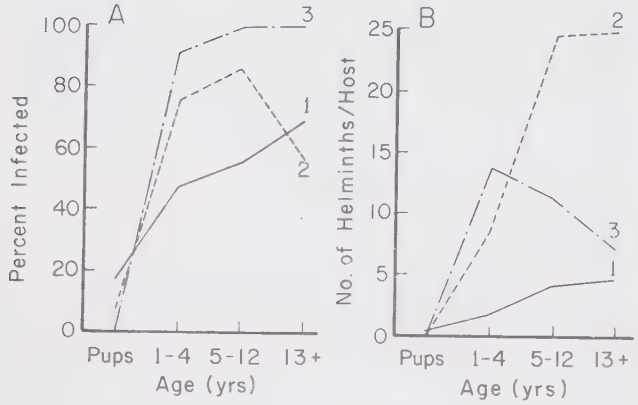


Figure 2.—Percentage of seals infected (A) by *Corynosoma semerme*, and mean numbers per host (B) in relation to age of spotted seals taken in the Karaginskii (1), Anadyr (2), and Pribilof (3) regions of the Bering Sea.

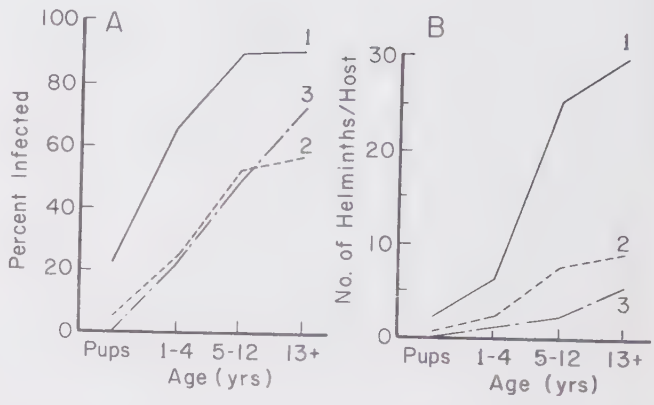


Figure 3.—Percentage of seals infected (A) by *Terranova azarasi*, and mean numbers per host (B) in relation to age of spotted seals taken in the Karaginskii (1), Anadyr (2), and Pribilof (3) regions of the Bering Sea.

The seals from the southeastern Bering Sea differed from the others in that they alone had the trematode *Microphallus orientalis*, the acanthocephalan *Bolbosoma* sp. (footnote 6), the cestode *Pyramicocephalus phocarum*, and the nematode *Otostrongylus circumlitus*. Only the Karaginskii seals had the trematode *Orthosplanchnus pygmaeus*, and only they and the Navarin-Anadyr seals had the acanthocephalan *Corynosoma wegeneri* and nematodes identified as *Terranova decipiens* and *Parafilaroides krascheninnikovi*.

Quantitative comparison between regional samples could be done only with the species of helminths which they had in common. Those, of course, were the ones which most frequently and most intensively infected these seals. The data obtained indicate substantial differences in frequency of occurrence of the helminths between samples (Table 1).

The southeastern and southwestern (Karaginskii) samples differed significantly to highly significantly in infection rate by four species [*Phocitrema fusiforme, Anophryocephalus* sp. (footnote 6), *Corynosoma semerme*, and *Anasakis simplex*]; the mean numbers per host (Table 2) also differed significantly to highly significantly for five species [*Anophryocephalus skrjabini* (footnote 6), *Corynosoma semerme, C. strumosum, Anasakis simplex*, and *Terranova azarasi* (footnote 6)]. Significant differences in infection rate were not indicated for the cestode *Diplogonoporus tetrapterus*; the acanthocephalans *Corynosoma strumosum, C. validum*, and *C. villosum*; or for the nematodes *Phocascaris cystophorae, Terranova* sp. (footnote 6), and *Dipetalonema spirocauda*. Most of those [excepting *C. strumosum* and *T. azarasi* (footnote 6)] also did not differ significantly in numbers per host.

The helminth fauna of the sample from the southeastern Bering Sea also differed significantly to highly significantly from that of the Navarin-Anadyr sample in infection rate by nine species of helminths [*Orthosplanchnus arcticus, Phocitrema fusiforme, Anophryocephalus* sp. (footnote 6), *Corynosoma semerme, C. strumosum, Contracaecum osculatum, Phocascaris cystophorae, Terranova* sp. (footnote 6), and *Dipetalonema spirocauda*]. For only *P. cystophorae*, however, did the numbers per host differ significantly.

Some differences between regional samples also were apparent in the species diversity of helminths in seals of different age classes (Table 3). The clearest tendency toward increased diversity in relation to the age of the hosts was evident in the seals from the southeastern Bering Sea. In the Anadyr sample, conversely, a tendency toward diminution in number of species was indicated in the oldest age group of seals. The coefficient of variation of species diversity also was least overall (35.9%) in the southeastern sample and lower for each age group than in the other regional samples.

DISCUSSION

The great similarity between the three samples of seals in the composition of their helminth faunas indicates a high degree of uniformity in the diets of the spotted seals in all regions. The greater similarity in some respects between the helminths of the southeastern and Karaginskii seals than between those of the southeastern and

Navarin-Anadyr concentrations is notable and may be attributable to the greater similarity of habitats occupied by the seals in Karaginskii Gulf and the Pribilof-Bristol Bay regions, with consequent availability of similar, subarctic prey. The waters of the Navarin-Anadyr region, conversely, are appreciably deeper and colder than those of the southeastern and southwestern shelves of the Bering Sea and support a predominantly arctic assemblage of organisms (Zenkevitch 1963).

Although the availability to the seals of somewhat different assemblages of prey in each of the three regions may account for some of the difference between their helminth faunas, other factors such as prey selection may be of equal or greater importance. That is, the spotted seals inhabiting each region may exhibit learned, traditional, or inherited preferences for different kinds or sizes of prey than those in the other regions, the result of which could be infection by different kinds and numbers of helminths. That this is a plausible factor is suggested by the distinct differences in helminth faunas between the southeastern Bering Sea spotted seals and their sympatric relatives, the Pacific harbor seals, *Phoca vitulina richardsi*, of the Pribilof Islands (Shults 1979,[7] 1982). The same kinds of prey were available to both species of seals at the same time (April) and some of those were eaten by both species (Lowry and Frost 1981). Nevertheless, the harbor and spotted seals were infected in common by only six species of helminths [*Anophryocephalus* sp. (footnote 6), *Diplogonoporus tetrapterus, Corynosoma semerme, C. strumosum, Contracaecum osculatum*, and *Dipetalonema spirocauda*]. The infection rates by each helminth also were markedly different in the two species of seals. Furthermore, the harbor seals lacked the other 12 species which were present in the spotted seals and were infected by one (*Corynosoma hadweni*) which was absent from the spotted seals. The contrasting results indicate that these two closely related species of seals, given access to the same food sources, have somewhat dissimilar dietary preferences as a consequence of learned or inherited behaviors. We suggest that the same may be true of the spotted seals in the three areas where breeding is concentrated. Since each is genetically differentiated to some degree, as indicated by their craniological variation (Fedoseev 1984), a corollary may be behavioral differentiation.

In our opinion, the helminthological findings reported here lend some support to the concept of three semidiscrete subpopulations of spotted seals in the Bering Sea, as has been indicated by the distributional and craniological data.

[7]Shults, L. M. 1979. Helminth parasites of the Pacific harbor seal, *Phoca vitulina richardsi*, from Alaskan waters. Unpubl. manuscr., 10 p. Institute of Marine Science, University of Alaska, Fairbanks, AK 99701.

ACKNOWLEDGMENTS

We wish to thank Robert L. Rausch, Murray D. Dailey, and Carol A. Nielsen who read and commented on an earlier draft of this report. Support for our work was provided in part by the Pacific Research Institute of Fisheries and Oceanography, U.S.S.R. Ministry of Fisheries, and the Frunze State University (Delyamure, Yurakhno, Popov), and in part by the U.S. Bureau of Land Management through interagency agreement with the National Oceanic and Atmospheric Administration, as a part of the Outer Continental Shelf Environmental Assessment Program (Shults and Fay).

LITERATURE CITED

BEKLEMISHEV, V. N.
1970. Population biology as one of the theoretical bases for mosquito control. *In* Biocenological basis of comparative parasitology, p. 202-214. Nauka, Moscow.

BRAHAM, H. W., J. J. BURNS, G. A. FEDOSEEV, and B. D. KROGMAN.
1984. Habitat partitioning by ice-associated pinnipeds: Distribution and density of seals and walruses in the Bering Sea, April 1976. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:25-47.

BREEV, A. K.
1976. Applications of mathematical methods in parasitology. Izv. GOSNIORKH 105:109-126.

CHAPSKII, K. K.
1969. Taxonomy of seals of the genus *Phoca sensu stricto* in the light of contemporary craniological data. *In* V. A. Arsen'ev, B. A. Zenkovich, and K. K. Chapskii (editors), Marine mammals, p. 294-304. Nauka, Moscow.

DELYAMURE, S. L., M. V. YURAKHNO, and V. N. POPOV.
1979. Composition of helminths as a population marker in seals. Priroda 1979(5):111-113.

FEDOSEEV, G. A.
1984. Use of nonmetrical characters of skulls of Bering Sea seals in a study of the phenotypic structure of their populations. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:49-54.

GOL'TSEV, V. N., M. V. YURAKHNO, and V. N. POPOV.
1978. On the question of local Karaginskii and Anadyr populations of the Bering Sea larga. Zool. Zh. 57:280-287.

LOWRY, L. F., and K. J. FROST.
1981. Feeding and trophic relationships of phocid seals and walruses in the eastern Bering Sea. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: oceanography and resources, Vol. 2, p. 813-824. Univ. Washington Press, Seattle.

MOHR, E.
1965. Über *Phoca vitulina largha* Pallas, 1811 und weissgebörene Seehunde. Z. Säugetierkd. 30:273-287.

SHAUGHNESSY, P. D., and F. H. FAY.
1977. A review of the taxonomy and nomenclature of north Pacific harbour seals. J. Zool. (Lond.) 182:385-419.

SHULTS, L. M.
1982. Helminths of the spotted seal, *Phoca largha*, from the Bering Sea. J. Wildl. Dis. 18:59-62.

TIKHOMIROV, E. A., and G. M. KOSYGIN.
1966. Prospects for commercial sealing in the Bering Sea. Rybn. Khoz. 8:25-28.

ZENKEVITCH, L.
1963. Biology of the seas of the U.S.S.R. Wiley-Interscience, N.Y., 955 p.

Abundance and Distribution of the Pacific Walrus, *Odobenus rosmarus divergens*: Results of the First Soviet-American Joint Aerial Survey, Autumn 1975

JAMES A. ESTES[1] and VITALI N. GOL'TSEV[2]

ABSTRACT

An aerial survey of the Pacific walrus, *Odobenus rosmarus divergens*, coordinated between the Soviet Union and the United States, was carried out during autumn 1975. Purposes of the survey were to estimate walrus abundance and distribution, and to evaluate aerial survey methods. Biologists from the United States surveyed the edge of the pack ice from Pt. Barrow west to long. 174°W. Biologists from the Soviet Union surveyed coastal areas and the edge of the pack ice east to long. 178°W. Congregations of walruses on shore were counted from aerial photographs, the distribution and abundance of walruses hauled out on the pack ice were estimated from random and systematic aerial transects. Walruses were most abundant between about long. 162° and 165°W in the U.S. sector. Most of these animals were associated closely with the southern edge of the pack ice. The number of walruses hauled out and the frequency distribution of group size varied significantly among days. Abundance estimates in the U.S. sector ranged between about 2,500 and 100,000 animals. In the Soviet sector of the Bering and Chukchi Seas nearly 100,000 walruses were counted from photographs of coastal aggregations, and 26,000 were estimated from surveys of the pack ice. The number in the Bering Sea was greater than usual, possibly due to unusually heavy sea ice in the western Chukchi Sea. Although these and earlier data support the notion that the Pacific walrus population has increased in size in recent years, their substantial bias and variation contribute to unacceptably wide confidence limits on estimates of abundance and population trends.

РЕЗЮМЕ

Аеровизуальные наблюдения за тихоокеанским моржом, скоординированные между Советским Союзом и США, были выполнены осенью 1975 г. с целью изучения распределения, оценки запасов, а также апробирования разных способов аэроучета. Американские исследователи обследовали район кромки льда от мыса Барроу до 174° з.д.. Советские исследователи осмотрели прибрежные районы и кромку льда на востоке до 178° з.д.. Подсчёт моржей на лежбищах проводился по аэрофотоснимкам. Распределение и количество моржей на льду определялось бессистемно, а также по схеме на учетных полосах. Наибольшее количество моржей зарегистрировано между 162° з.д. и 165° з.д. в американском секторе. Эти звери в основном располагались вблизи южной кромки пакового льда. Количество моржей на льду, частота встречаемости стад и их величина значительно изменялись в отдельные дни. Численность зверей в американском секторе колебалось от 2,500 до 100,000 голов. В советском секторе Берингова и Чукотского морей около 100,000 голов подсчитаны по аэрофотографиям лежбищ; 26,000 подсчитаны по аэровизуальным наблюдениям на паковом льду. Количество моржей в Беринговом море было больше, чем обычно, что возможно связано с тяжелой ледовой обстановкой в западной части Чукотского моря.

Несмотря на то, что наши данные и более ранние исследования подтверждают мнение о росте популяции тихоокеанского моржа в последние годы, тем не менее нет большой уверенности в достоверности оценок численности и тенденции популяции ввиду широкой вариабильности данных.

INTRODUCTION

The Pacific walrus, *Odobenus rosmarus divergens*, is conspicuous and unique among ice-inhabiting pinnipeds of the Bering and Chukchi Seas. Walruses are closely associated with the southern part of the polar ice cap, and they migrate great distances in response to seasonal variation in the distribution of pack ice. During late winter, the population occupies the area from Bristol Bay (Fig. 1) northwestward to Anadyr Gulf. Walruses migrate through Bering Strait in spring. By late September, when the pack ice has receded into the Arctic Ocean, walruses are found along the ice edge from about Point Barrow westward to the mouth of the Kolyma River in the East Siberian Sea. At least 6,000 to 8,000 males remain throughout the summer in Anadyr Gulf at Rudder and Meechken Spits, and at least 12,000 remain in Bristol Bay at Round Island (Gol'tsev 1968; Taggart and Zabel 1980[3]).

During summers when the weather is warm and the edge of the pack ice is far north (to lat. 73° or 74°N), walruses abandon the pack ice and haul out on Wrangel and Herald Islands and at a number of locations along the northern coast of the Chukchi Peninsula. During cooler summers, when the ice edge is farther south, they remain with the ice rather than coming ashore (Tomilin and Kibal'chich 1975). Formation of new ice begins in Long Strait during early October and the walruses begin to migrate southeastward toward Bering Strait. When there is no sea ice along their migration route, they haul out to rest on the northern coast of the Chukchi Peninsula

[1]U.S. Fish and Wildlife Service, Denver Wildlife Research Center, Center for Marine Studies, Applied Sciences Building, University of California, Santa Cruz, CA 95064, USA.

[2]Magadan Branch, Pacific Research Institute of Fisheries and Oceanography (MoTINRO), Nagaevskaya 51, Magadan 685013, USSR.

[3]Taggart, S. J., and C. Zabel. 1980. Round Island report, summer 1980. Unpubl. rep., 13 p. Alaska Dep. Fish Game, Dillingham, AK 99576.

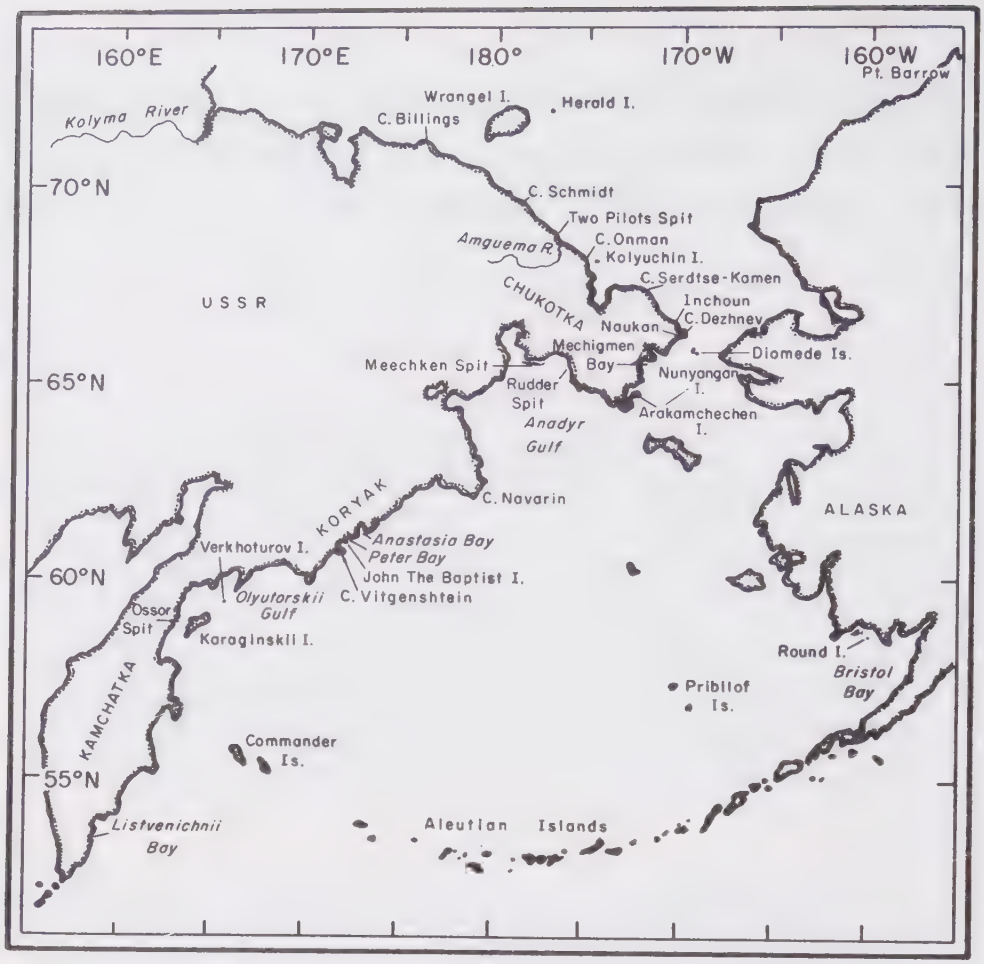


Figure 1.—The Soviet Far Eastern Coast, showing places referred to in this report.

(Nikulin 1947). The peculiarities of this distribution and of the behavior of walruses in autumn can be used advantageously to census a substantial portion of the total population directly.

Before about the middle of the 19th century the Pacific walrus population had been little affected by human exploitation, although walruses had been harvested for at least 2,500 yr by Eskimos. During the last half of the 19th century, the walrus population declined in abundance and range as a consequence of commercial harvesting by Yankee whalers (Fay 1957). By the beginning of the 20th century, those harvests had decreased to a low level, and practically ceased during World War I. Commercial harvests of walruses were taken by the Soviet Union from 1930 to 1957. By the late 1950's, both the USA and the USSR had forbidden the harvest of walruses except for subsistence use by local people.

Research on the natural history and population status of the Pacific walrus began in Alaska and Chukotka in the 1930's (Belopol'skii 1939; Collins 1940) and was intensified in the 1950's (Brooks 1954; Fay 1955; Fedoseev 1962; Krylov 1962). In 1958 the State of Alaska and the Soviet Government initiated management programs based on the harvests of walruses by natives in Alaskan and Far Eastern waters (Burns 1965;[4] Krylov 1968). Aerial surveys to determine the abundance of walruses were begun by the Soviet Union in 1958 (P. G. Nikulin *in* Fedoseev 1962) and by the United States in 1960 (Kenyon 1960[5]). Later, surveys were conducted by the Soviet Union in 1960, 1964, and 1970, and by the United States in 1961, 1968, and 1972. The results of those surveys suggested that walruses were increasing in abundance, though the basis for that conclusion was weak because some portions of the area occupied by walruses were not surveyed.

This paper reports the results of an internationally coordinated aerial survey of the Pacific walrus. The accuracy and precision of the population estimates derived from it are discussed and the utility of aerial surveys for future studies of walruses is considered.

METHODS

During June 1975, scientists from the United States and Soviet Union met in Leningrad to discuss procedures whereby the joint survey of walruses would be carried out. Agreement was reached on beginning the survey in early September, the exact time depending on availability of aircraft. The boundary between the American and Soviet survey areas would be the International Date Line. Because the problems associated with surveying walruses in the pack ice differ from those in surveying coastal haul out areas, methods employed by the United States and the Soviet Union are discussed separately.

[4]Burns, J. J. 1965. The walrus in Alaska, its ecology and management. Alaska Dep. Fish Game, Juneau, 48 p.

[5]Kenyon, K. W. 1960. Aerial surveys of marine mammals in the Bering Sea, 23 February to 2 March 1960 and 25-28 April 1960. Unpubl. rep., 39 p. U.S. Bur. Sport Fish. Wildl., Seattle, WA 98115.

American Survey

The survey was carried out along the ice edge zone of the eastern Chukchi Sea, between Point Barrow and the International Date Line. The northern boundary of the survey area was about 50 nmi (93 km) north of the ice edge; the southern boundary was at lat. 69°30′N and the Alaskan coastline. The southern boundary at lat. 69°30′N was about 100 nmi (185 km) south of the ice edge. We assumed that most walruses in the open water south of the pack ice would occur within that range.

We allocated 4 d of our survey effort to the pack ice zone and 1 d to the expanse of open water south of the ice edge. The survey strips were selected at random each day from a set of 360 potential north-south transects, 1 nmi (1.85 km) apart. These were located between long. 156° and 174°W. For surveys over the ice zone, each survey strip crossed the area between the consolidated pack and the southern extremity of dispersed drifting ice. The northern and southern ends of those strips were predetermined each day, on the basis of ice information provided by the U.S. Navy Fleet Weather Facility and our observations from the previous day's survey.

The survey aircraft was a Lockheed P2V[6] equipped with a Global Navigation System and long range fuel capacity. This aircraft was selected because it afforded excellent air to surface visibility from the nose bubble. It was flown at a speed of 150 nmi/h (278 km/h) and at an altitude of 500 ft (152 m), except where the cloud ceiling required a lower altitude for adequate visibility. Two observers counted the animals along a strip extending 0.5 nmi to each side of the flight track. We counted each walrus or group of walruses; the number of animals per group was counted or estimated. A group was defined as two or more walruses within about one body length of each other. Animals within the 0.5 nmi (0.93 km) wide transect on each side of the flight track were classified further as occurring 1) within the inner 0.125 nmi (0.23 km), 2) between 0.125 and 0.25 nmi (0.46 km), or 3) between 0.25 and 0.5 nmi from the flight track. We determined those distances by sighting along the appropriate angles marked on protractors mounted at eye level on each side of the nose bubble. Angles were adjusted for changes in altitude.

Each day, 9 to 14 strips were surveyed. On 9 September, however, we terminated the survey after 7 strips, because of equipment failure. The number of strips per day was determined by the maximal range of the aircraft and the location of each transect. By this means, we obtained random samples of the distribution and abundance of the walruses visible to us within the survey areas.

Soviet Survey

Walruses in the Bering and Chukchi Seas west of the International Date Line were surveyed via an IL-14 aircraft between 15 September and 16 October. In that area, walruses occur in large numbers both on the pack ice and on coastal hauling grounds.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

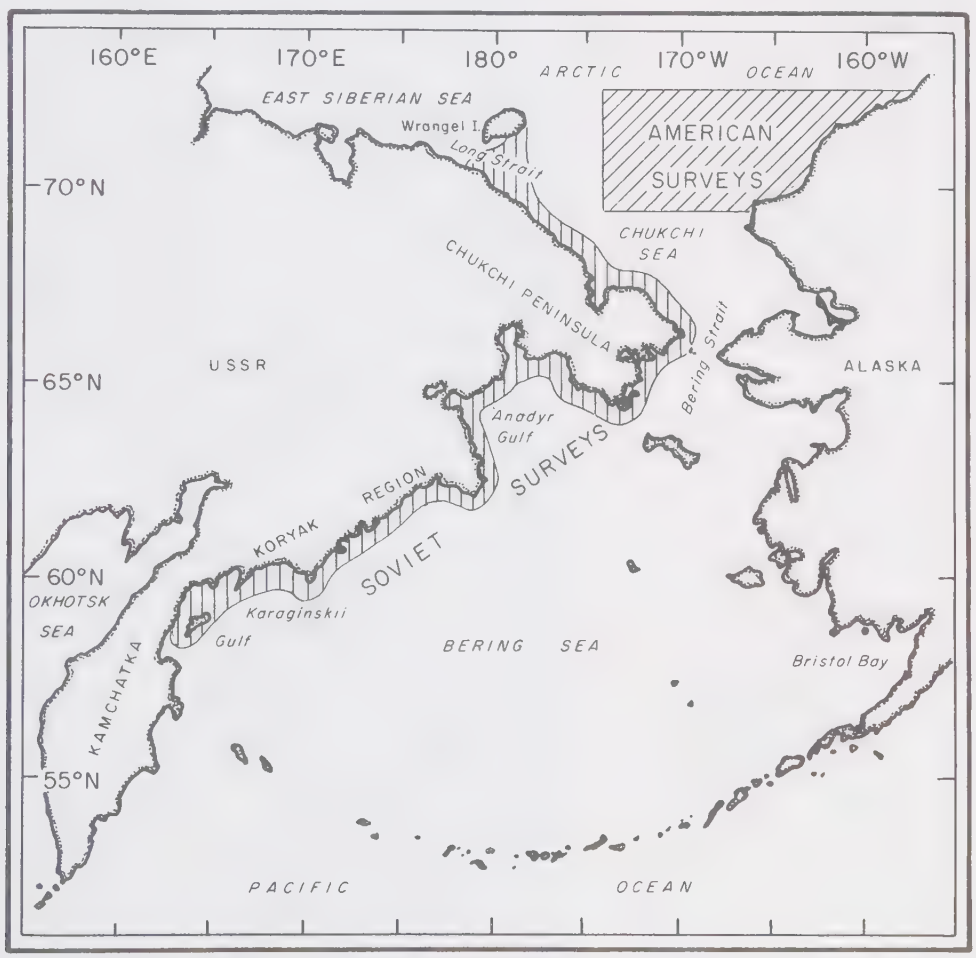


Figure 2.—Major features of the Bering-Chukchi region, showing the areas surveyed in this study.

The shoreline was surveyed from Ossor Spit and Karaginskii Island, southwestern Bering Sea, to Cape Schmidt and western Chukchi Sea (Fig. 2). The larger groups of walruses were photographed from directly overhead (Fig. 3) at an altitude of 700 to 1,000 m (depending on ceiling), with a linear overlap between adjacent frames of 30 to 35%. The areas occupied by walruses on the photographs were measured with a planimeter, and the density of animals was determined by sample counts with a binocular magnifier. With these data, the total number of walruses occupying the hauling ground was estimated. In areas where density varied over the hauling ground, walruses were counted individually, as were those nearby in the water. We found that extrapolated estimates varied from exact counts by less than ± 2.5%.

Reconnaissance flights were flown initially over the pack ice to determine the distribution of walruses and ice conditions. Systematic transects were flown on subsequent days over the areas in which walruses had been seen. The distance between adjacent transects varied from 10 to 20 km. Estimates of abundance were based on the area sampled and walrus density. We have no reason to believe that the different methods we employed in surveys over the ice were of any real consequence to our results.

The aircraft was flown at an average speed of 250 km/h. Width of the transect was estimated from angles marked on the viewing port. The plane was equipped with two cameras: An AFA-TE-500, 18 × 18 cm format, with a 500 mm objective lens, and an AFA-42-20, 30 × 30 cm format, with a 200 mm objective lens. From an altitude of 1,000 m, these camera systems provide respective scales of 1/2,000 and 1/5,000. The AFA-42-20 was operated simultaneously only when there were many walruses in the water that could not be photographed by the AFA-TE-500.

RESULTS

American Survey

The ice edge east of the International Date Line drifted in a generally southward direction from 1 September when the surveys began, to 12 September when they were completed. This movement was as great as 139 to 185 km in some areas. The ice edge was convoluted in the vicinity of the International Date Line, crossing the Date Line at several locations.

Walruses were most abundant between about long. 162° and 165°W (Fig. 4). Large numbers of animals were observed in all ice concentrations (Estes and Gilbert 1978). Of 3,572 walruses sighted in the sample strips from the ice edge northward, 3,522 (98.6%) were situated in the southernmost 6 deciles of the transects (Fig. 5A), compared with an expected 2,143 (60%) if the distribution had been uniform. These data suggest that our survey area over the ice

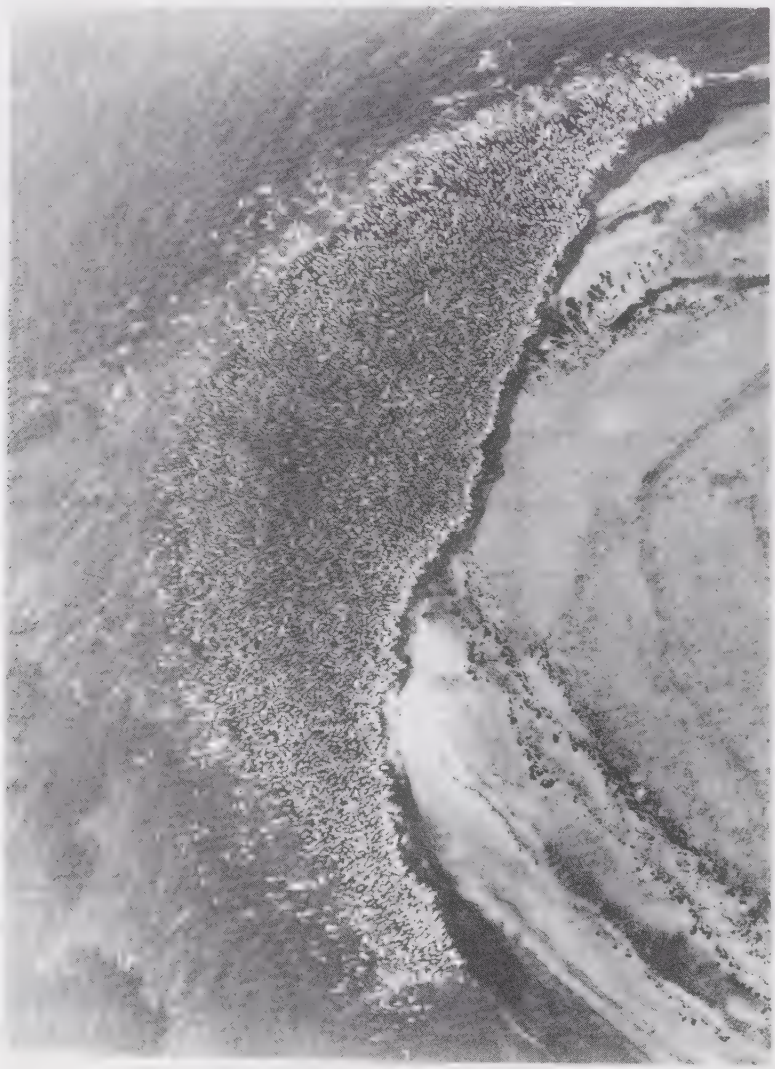


Figure 3.—Aerial photograph of walruses on hauling ground at Meechken Island, 18 September 1975.

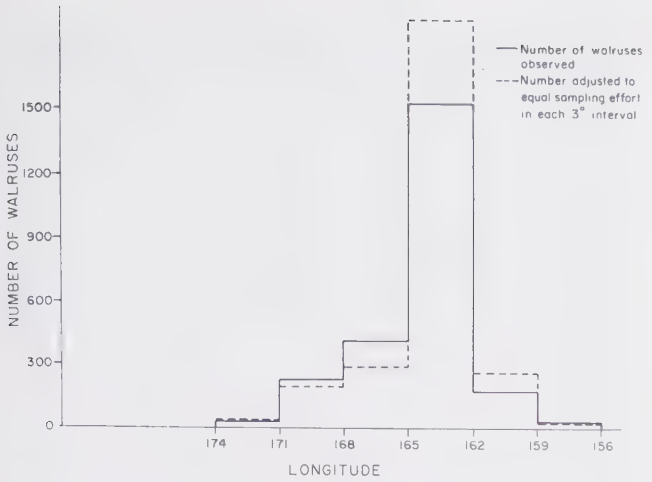


Figure 4.—The number of walruses observed (solid line) within longitudinal intervals of 3° along the ice edge of the eastern Chukchi Sea. Only data from 5, 8, and 12 September 1975 are included. Numbers were adjusted (dash line) by multiplying by $\bar{n}/n_i$ where n_i = the number of strip samples taken from the ith interval of 3° longitude and $\bar{n}$ = the mean of these values (after Estes and Gilbert 1978).

sampled most of the walruses which were associated with the pack ice. The distributional pattern of animals in the open water south of the ice was more irregular (Fig. 5B). Hence, our survey area there may have been too small by limiting its southward extent to lat. 69°30′N. This suggestion is partly negated by the fact that the number of animals seen in the open water survey was very small.

The numbers of walruses counted on ice and in the water in the three subtransects (i.e., 0 to 0.23 km, 0.23 to 0.46 km, and 0.46 to 0.93 km) on each side of the flight track are shown in Table 1. The probability of variation from a uniform distribution was tested by the χ^2 method. The results suggest that the probability of sighting walruses on the ice was nearly constant from 0 to at least 0.93 km (as was concluded also by Kenyon 1972[7]), whereas the probability of sighting walruses in the water decreased at distances > 0.23 km. For a more detailed discussion of this, see Estes and Gilbert (1978:1113-1114).

[7]Kenyon, K. W. 1972. Aerial surveys of marine mammals in the Bering Sea, 6-16 April 1972. Unpubl. rep., 79 p. U.S. Bur. Sport Fish. Wildl., Seattle, WA 98115.

Table 1.—Chi-squared tests of goodness of fit of sighted, as compared with expected (uniform), distribution of walruses in relation to distance from the aircraft.[1]

	Distance from flight track (km)			
	0-0.23	0.23-0.46	0.46-0.93	χ^2
Groups on ice				
Sighted	31	41	80	1.7
Expected	38	38	76	
Individuals on ice				
Sighted	442	944	2,323	[2]372.5
Expected	927	927	1,854	
Groups in water				
Sighted	26	17	13	[2]18.9
Expected	14	14	28	
Individuals in water				
Sighted	68	53	39	[2]42.6
Expected	40	40	79	

[1]From American survey only.
[2]$P(\chi^2_2 > 9.2) = 0.01$.

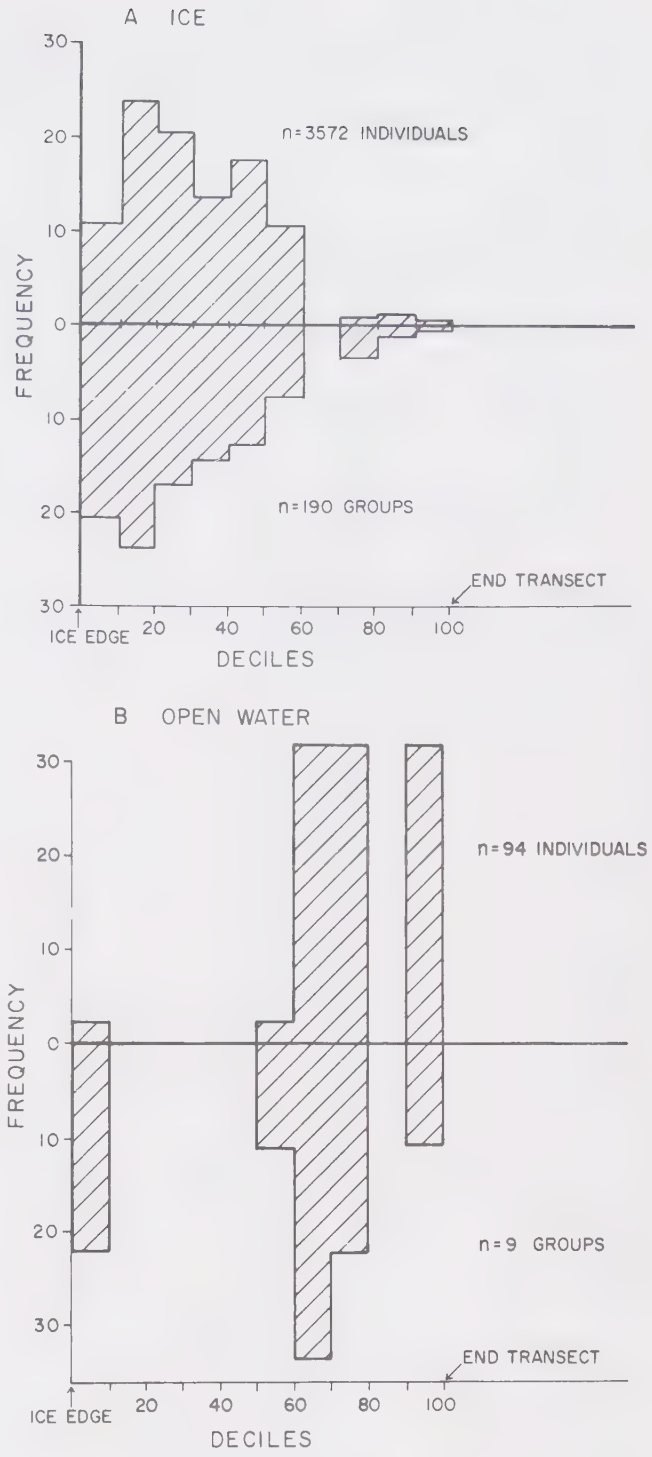


Figure 5.—Frequency distributions of the numbers of individuals and numbers of groups of walruses sighted within decile segments of the survey strips, A) from the ice edge northward, and B) from the ice edge southward in the Chukchi Sea, 5-12 September 1975 (after Estes and Gilbert 1978).

The total number of groups sighted on 8 September was an order of magnitude greater than the number sighted on any of the other 3 d of over-ice surveys (Table 2). Furthermore, in the over-ice surveys the number of walruses sighted in the water versus on the ice each day differed highly significantly from the expected (overall mean) number ($\chi^2_3 = 208.56$; $P < 0.01$). The same

Table 2.—Summary of counts of walruses from the American surveys in the eastern Chukchi Sea, 1975.[1]

Date, location, and no. of strips (n)	Number of groups		Number of individuals	
	On ice	In water	On ice	In water
1 Sept., over water (10)				
Total	—	21	—	42
Mean/strip	—	2.1	—	4.2
5 Sept., over ice (9)				
Total	10	12	106	19
Mean/strip	1.1	1.3	11.8	2.1
8 Sept., over ice (14)				
Total	118	22	3,150	63
Mean/strip	8.4	1.6	225.0	4.5
9 Sept., over ice (7)				
Total	18	9	161	38
Mean/strip	2.6	1.3	23	5.4
12 Sept., over ice (13)				
Total	6	13	292	38
Mean/strip	0.5	1.0	22.5	2.9

[1]Summarized from Estes and Gilbert (1978).

comparison, tested without the data from 8 September, indicated no significant difference among days ($\chi^2_2 = 5.91$; $P > 0.05$). Thus, there is high probability that, not only was a much larger number present in the area on 8 September, but a much higher proportion of them was on the ice.

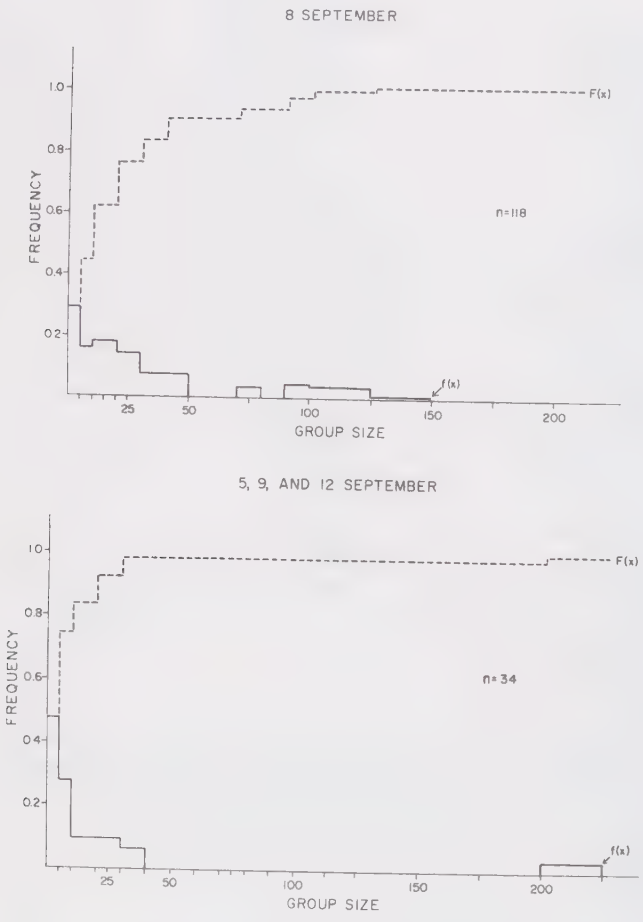


Figure 6.—Comparative frequency distributions of group sizes of walruses sighted on ice in the eastern Chukchi Sea, on 8 (upper) versus 5, 9, and 12 (lower) September 1975. Dash line F(X) shows the cumulative frequency distribution (after Estes and Gilbert 1978).

The frequency distribution of group sizes sighted indicated that a greater proportion of the animals was in large groups on 8 September than on the combined days of 5, 9, and 12 September (Fig. 6). On 5, 9, and 12 September, only a single group larger than 50 walruses and only 6 groups larger than 25 walruses were sighted (Fig. 6). On 8 September, 12 groups larger than 50 walruses and 62 groups larger than 25 walruses were sighted. The mean group size tended to be about 10 times greater on ice than in water.

We employed two methods to estimate the abundance of walruses in U.S. waters. Method I was a modified ratio of means estimator whereby the sample density of walruses was multiplied by the area surveyed. Method II was independent of area, treating each sample transect as a random sample of the ice between long. 156° and 174°W. Essentially, Method II transformed the sample space into a single dimension which was divided into equal sampling intervals, each 1.85 km in length. Both methods were modified to obtain estimates based on the product of group density (or number for Method II) and mean group size. A variance was calculated for each population estimate (Estes and Gilbert 1978).

Estimates of walrus abundance ranged between 818 and 1,621 in the open water and between 2,475 and 100,568 in the ice. Coeffi-

Table 3.—Estimates of the total abundance ($\hat{T}$) and standard deviation $S(\hat{T})$ of walruses in the eastern Chukchi Sea, based on the American surveys in 1975.

Date, location, and method of estimation	Estimated abundance			
	Based on number of individuals		Based on number of groups and mean group size	
	$\hat{T}$	$S(\hat{T})$	$\hat{T}$	$S(\hat{T})$
1 Sept., over water				
Method I[1]				
All strips	818	684	818	665
N-S strips only	1,581	1,309	1,621	1,348
Method II[2]				
All strips	1,026	927	1,026	954
N-S strips only	1,716	1,696	1,760	1,740
5 Sept., over ice				
Method I				
All strips	2,475	1,606	2,475	2,170
N-S strips only	4,656	2,846	4,224	4,094
Method II				
All strips	5,000	2,737	5,000	2,871
N-S strips only	8,568	4,480	7,773	4,650
8 Sept., over ice				
Method I				
All strips	75,959	30,921	75,959	19,121
N-S strips only	100,568	57,689	85,848	29,222
Method II				
All strips	82,620	37,428	82,620	26,020
N-S strips only	90,765	63,561	77,480	33,007
12 Sept., over ice				
Method I				
All strips	7,755	4,551	7,755	5,920
N-S strips only	13,533	7,990	11,587	9,259
Method II				
All strips	9,138	6,130	9,138	6,743
N-S strips only	12,780	9,915	10,942	8,402
Combined, over ice, all days				
Method I				
All strips	27,000	10,731	27,000	7,097
N-S strips only	36,337	20,616	32,871	11,511
Method II				
All strips	36,680	15,127	36,680	10,191
N-S strips only	41,486	24,551	37,528	12,937

[1]Mean density per survey, extrapolated to total area. "All strips" include the north-south strips, as well as the diagonals between them.

[2]Mean number per strip, times the total number of possible strips.

cients of variation [$S(\hat{T})/\hat{T}$, where $\hat{T}$ = estimated size of the population and $S(\hat{T})$ = standard deviation of estimated population size] ranged between 0.26 and 0.99 (Table 3, mean = 0.62).

Soviet Survey

The coast of Siberia from Ossor Spit and Karaginskii Island, eastern Kamchatka, to Kolyuchin Island in the Chukchi Sea, and the ice edge from Cape Billings to Wrangel Island (Fig. 2) were surveyed during reconnaissance flights on 17 and 19 September and 5 October. Coastal hauling grounds were identified in the Bering Sea on John the Baptist Island, the western extremity of Meechken Spit, Rudder Spit, Nunyangan Island, Arakamchechen Island, the eastern end of Big Diomede Island, and near the former village site of Naukan. In the Chukchi Sea, coastal hauling grounds were located at Cape Inchoun and Cape Serdtse Kamen.

About 77,000 and 20,000 walruses were counted from photographs taken of coastal hauling grounds in the Bering and Chukchi Seas, respectively (Table 4). The large numbers of walruses usually found on or near Wrangel Island in September apparently were farther south, because of unusually heavy ice in the western Chukchi Sea. The number in the Bering Sea was much larger than usual,

Table 4.—Number of walruses counted and estimated on coastal hauling grounds along the Soviet Coast, September-October 1975.

Date	Time	Weather	Number of walruses	Area occupied per walrus (m^2)	Basis
John the Baptist Island					
4 Oct.	1313	Overcast, calm	200	4	Individual count.
Meechken Spit					
18 Sept.	1007	Clear, calm	8,242	1.8	Extrapolated from density and area.
18 Sept.	1007	Clear, calm	8,044	1.8	Individual count.
21 Sept.	1547	Clear, light wind	500-600	—	Visual estimate.
Rudder Spit					
21 Sept.	1533	Clear, light wind	445	—	Individual count.
Nunyangan Island					
18 Sept.	1153	Overcast, stormy	1,152	—	Individual count.
19 Sept.	0955	Overcast, windy	627	—	Individual count.
21 Sept.	1412	Clear, light wind	19,977	1.54	Extrapolated from density and area.
9 Oct.	1033	Overcast, windy	1,628	—	Individual count.
Arakamchechen Island					
18 Sept.	1215	Overcast, stormy	3,996	1.89	Extrapolated from density and area.
19 Sept.	1007	Overcast, windy	1,208	—	Individual count.
21 Sept.	1400	Clear, light wind	41,882	1.56	Extrapolated from density and area, and individual count.
9 Oct.	1050	Overcast, windy	—	—	Several thousand sleeping in the water.
Big Diomede Island					
21 Sept.	1132	Clear, light wind	4,228	2.43	Individual count.
21 Sept.	1146	Clear, light wind	3,516	—	Individual count.
Naukan					
21 Sept.	1132	Clear, light wind	2,144	1.76	Extrapolated from density and area, and individual count.
5 Oct.	1233	Clear, calm	2,326	—	Walruses approaching from the north.
7 Oct.	1146	Clear, light wind	2,417	1.32	Many walruses in the water.
9 Oct.	1150	Overcast, windy	3,357	1.88	Walruses approaching from the north.
Inchoun					
21 Sept.	1115	Clear, light wind	5,029	1.70	Extrapolated from density and area, and individual count.
5 Oct.	1246	Clear, calm	7,742	1.67	Extrapolated from density and area, and individual count.
7 Oct.	1132	Clear, windy	3,700	1.30	Extrapolated from density and area, and individual count.
9 Oct.	1202	Light clouds, calm	5,700	—	Individual count.
Cape Serdtse Kamen					
5 Oct.	1320	Clear, calm	11,972	1.95	Extrapolated from density and area, and individual count.
9 Oct.	1245	Clear, calm	9,188	2.83	Extrapolated from density and area, and individual count.

possibly for the same reason. For example, during September 1970, only 20,000 walruses were observed on coastal hauling grounds in the Bering Sea (Gol'tsev 1972[8]).

Walrus hauling grounds on John the Baptist and Nunyangan Islands were recorded for the first time during the autumn of 1975. Those animals on John the Baptist Island apparently are part of a small herd that has remained in the vicinity of Peter and Anastasia Bays and in Olyutorskii Gulf, during the past several summers. V. V. Zimushko[9] saw 12 walruses 11 to 15 km off the coast of Anastasia Bay, 3 walruses near Cape Vitgenshtein, and 5 walruses about 59 km east of Cape Navarin. These animals probably all belonged to the group that summers in the Koryak region. Walruses that hauled out on Nunyangan Island may have occupied the Akkaniiskii hauling ground during earlier years. Up to 12,000 animals were observed by Gol'tsev at Cape Kriguigan on the Akkaniiskii hauling ground during autumn of 1972, 1973, and 1974; however, in 1975 this area was not occupied.

Most of the walruses associated with the ice edge during September were concentrated about 15 to 19 km east of Cape Billings and in a narrow strip of ice which extended from Kolyuchin Island to the Two Pilots Spit. Smaller numbers of walruses were seen from Cape Billings southeastward to the edge of the ice.

The ice edge in Long Strait during September 1975 was 140 to 157 km farther east than usual. The ice coverage also was greater than usual. During most years, ice conditions are less severe, and large concentrations of walruses occur in the area west and southwest of Wrangel Island, some 296 to 352 km north of their location in 1975.

Many small polynas were present near Cape Billings. Small groups of walruses (3 to 5 animals), frequently including females with calves, were observed moving in a southeasterly direction. From Cape Billings to long. 178°W, a density of 0.76 walruses/km^2 was observed, from which we estimated an overall abundance of 65,000 animals in that area. The density of walruses between the mouth of the Amguema River to Cape Onman was 16.4/km^2, which gave an abundance estimate in that area of 23,000 animals. Because most animals seen were in the water, these estimates probably were conservatively biased. The area of heavy ice west of Cape Billings was not surveyed; there was no ice along the coast southeast of Kolyuchin Bay, and walruses were not sighted in the water in that area.

The weather turned very cold in mid-September, and we expected this to speed up ice formation in the Chukchi Sea, forcing the walruses to migrate southeastward and to occupy shore hauling grounds earlier than usual. However, a storm passed over the Chukchi Peninsula in late September breaking up the eastern edge of the pack ice and driving the ice front 93 to 185 km westward, about to the longitude of Cape Schmidt. On 5 and 6 October, walruses were observed in the pack ice 9 to 15 km north of Cape Schmidt, but the general distributional pattern along the northern coast was unchanged from that observed in September. We estimated 26,000 walruses in the ice, about 20,000 of which were concentrated in two areas totaling 480 km^2.

We estimated walrus abundance in the Soviet sector from data obtained from the Chukchi Sea on 5 and 6 October and from the Bering Sea on 18 and 21 September, because the highest counts were obtained on those days. Those data provided an estimate of 128,000 to 130,000 walruses west of the International Date Line (Table 5).

Table 5.—Summary of numbers of walruses on coastal hauling grounds and on the ice in the Soviet sector, based on aerial surveys in 1975.

Location	Date	Time of day	Number of walruses
On coastal hauling grounds			
John the Baptist Island	4 Oct.	1313	220
Meechken Spit	18 Sept.	1007	8,242
Rudder Spit	21 Sept.	1533	445
Nunyangan Island	21 Sept.	1412	19,977
Arakamchechen Island	21 Sept.	1400	41,882
Big Diomede Island	21 Sept.	1142	4,228
Naukan	21 Sept.	1132	2,144
Inchoun	5 Oct.	1245	7,742
Cape Serdtse Kamen	5 Oct.	1315	11,972
On ice floes			
Cape Billings to Kolyuchin Island	5-6 Oct.	—	26,600
In water			
Mechigmen Bay	21 Sept.	1350	5,500
Cape Dezhnev to Cape Serdtse Kamen	5 Oct.	1235-1315	1,500
Grand total			130,452

Combined with results obtained in the U.S. sector, a total population of roughly 140,000 to 200,000 walruses was estimated.

DISCUSSION

Pacific walruses have been exploited in rather large numbers in the past by both the United States and the Soviet Union. There is still a substantial take in both countries. Furthermore, walrus habitat may be affected eventually by commercial developments, such as hydraulic dredging for bivalve mollusks and petroleum extraction from the continental shelf. Although the effects of those activities are uncertain, they could act to the detriment of the walrus population. In view of those potential difficulties, a reliable means of censusing the walrus population is of considerable importance to both the United States and the Soviet Union.

Aerial surveys provide information on the abundance and distribution of the population. The reliability of estimates of those two parameters is affected by both precision and bias in the surveys. The relative importance of precision and bias in estimates of abundance and distribution is quite different for walruses on coastal hauling grounds than for walruses in the pack ice.

The difficulties encountered in censusing walruses in the pack ice have been discussed in detail by Estes and Gilbert (1978); we present only a summary of that discussion here. The major problems in interpreting the survey data are that an unknown fraction of the population is visible at any given time, and the animals tend to congregate in several spatial scales. These sources of bias and imprecision cannot be separated. The number of walruses hauled out on the pack ice probably changes considerably with time, but we cannot determine with certainty that this was the cause of the high variation among days for the population estimates in the ice edge. Although the population estimate probably is conservative, it must be based on the pooled data from all days in which the survey was carried out. Because the coefficient of variation of the estimates ranged from 0.26 to 0.99, however, the lower bounds of 95% confidence limits around the estimates were between 0 and about 50% of the mean. The unfortunate result of this situation is that no estimate of the walrus population in the pack ice can be defended on scientific grounds much beyond the maximum actually counted.

For walruses on shore, censusing is somewhat less problematic because large numbers of animals can be counted directly. The

[8]Gol'tsev, V. N. 1972. Distribution and assessment of numbers of the Pacific walrus in the autumn of 1970. Abstracts 5th all-union conf. stud. marine mammals 1:25-28. Makhachkala.

[9]V. V. Zimushko, Fisheries Biologist, Pacific Research Institute of Fisheries and Oceanography, Nagaevskaya 51, Magadan 685013, pers. commun. August 1975.

primary requirement is to obtain the counts when the greatest numbers of walruses are hauled out. Since no estimates are made, sampling variation is not a problem. The major unanswered questions concerning the reliability of these counts are: 1) What fraction of the total number of walruses in the area were on shore at the time of the survey; 2) to what extent do walruses move between haul out areas in the time between surveys of separate areas; and 3) how many walruses were outside the surveyed areas? We doubt that the answer to the third question would have had any significant influence on our estimates because the walruses sighted were well within the boundaries of the areas surveyed. Also, the historical records of distribution of walruses in September-October show similar spatial distribution. If large numbers of animals ever occurred outside the areas surveyed, they probably would have been recorded in the historical data. The extent to which walruses moved between hauling areas, however, is unknown. Animals observed at Meechkin Spit on 18 September and at Inchoun and Cape Serdtse Kamen on 5 October could have been at one of the other hauling areas counted on 21 September, in which case they could have been counted twice. In view of the short distance between Inchoun and Cape Serdtse Kamen, the possibility that animals moved from one to the other during the time of the survey cannot be discounted. Also unknown is the fraction of walruses in a given area that is likely to be on shore at any particular time. Recent studies of walrus activity and behavior at Round Island in Bristol Bay have shown that the number of walruses on shore varies over about 10-d intervals by more than an order of magnitude; greatest numbers usually tend to be on shore for less than a day (Taggart and Zabel footnote 3). The proportion of walruses in the area which haul out on Round Island during this peak period remains unknown, but preliminary data from a small number of animals instrumented with radio transmitters indicate that it is less than unity (Taggart and Zabel footnote 3). These observations suggest that direct counts of walruses on shore are biased low, to an extent which probably varies from day to day.

In summary, the numbers of walruses sighted, both on the pack ice and on the shore, underrepresent to an unknown extent the numbers actually present in those areas. In the pack ice, this is complicated further by highly imprecise estimates of the numbers in the areas not surveyed. As a result, the only reliable numbers are of the animals actually counted; the statistical confidence in larger estimates of the population is extremely low. The true number of walruses must be greater than the number seen, but the magnitude of the difference remains unknown.

Interpretation of recent changes in the range of Pacific walruses presents similar difficulties, mainly due to year-to-year variation in the distribution of pack ice and the opportunistic manner in which most observations are made. In 1975, walruses were observed in Listvenichnyi Bay, Kamchatka. Small groups were seen also in Karaginskii Gulf, as well as on Verkhoturov Island, near the Commander Islands, and in the Okhotsk Sea. Also, several hauling grounds in the Bering Strait region which had not been occupied by walruses for many years were reoccupied. Although these observations suggest an increasing range of the population, they are complicated by the fact that the pack ice during the summer of 1975 remained unusually far south. In the southeastern Bering Sea, occasional walruses have been observed recently near coastal areas and at the mouths of major rivers in eastern Bristol Bay where they had not been reported previously. These observations might be interpreted as evidence of an expanding range but also could be ascribed to increased numbers of observers in those areas.

Despite those uncertainties, most available evidence suggests that the Pacific walrus population has increased over the past several decades (Table 6). Fay (1957) and Nikulin (*in* Fedoseev 1962) estimated that the number of walruses had declined to an all-time low of about 40,000-50,000 by the mid- to late 1950's. Various estimates by Fedoseev (1962), Kenyon (footnotes 5, 7), Burns (footnote 4), and Gol'tsev (footnote 8) suggested that the numbers increased subsequently. Although not much confidence can be placed in any of those numbers, the trend of increase probably is significant. We point out, however, that this conclusion is based largely on intuition, and we urge that it be used with caution.

Future research must address the question of walrus activity rhythms and movements, both at the level of the individual and the population. Such information would be useful for interpreting possible exchange of individuals among groups, and for estimation of the fraction of walruses that can be seen and counted at any particular time. Until studies of this sort are completed, reliable assessment of the actual abundance of the Pacific walrus population will remain an illusive goal.

Table 6.—Summary of population estimates of Pacific walruses from surveys during the past two decades.

Year	Population estimate (thousands)	Source
1950's	40-50	Fay 1957
1960	50	Fedoseev 1962
1960	78-113	Kenyon 1960[1]
1965	90	Burns 1965[2]
1970	101	Gol'tsev 1972[3]
1972	85-162	Kenyon 1972[4]
1975	140-200	This report

[1]See text footnote 5.
[2]See text footnote 4.
[3]See text footnote 8.
[4]See text footnote 7.

ACKNOWLEDGMENTS

This work was a collaborative effort carried out under auspices of the US-USSR Agreement on Cooperation in the Field of Environmental Protection. We thank the many people whose efforts in developing and implementing the Agreement made this work possible. James R. Gilbert helped with survey design and data analysis, and participated in the American survey. Various other individuals from TINRO (Magadan), Alaska Department of Fish and Game, National Marine Fisheries Service, Office of Aircraft Services (U.S. Department of the Interior), Naval Arctic Research Laboratory, and the U.S. Navy Fleet Weather Facility assisted us either as observers or through technical and logistic support. John J. Burns translated some of the work from Russian to English. Francis H. Fay reviewed and edited several earlier drafts of the manuscript, and helped with communication of information between us. Janet M. Pumphrey helped locate Russian place names. Financial support was provided by the Magadan Branch of TINRO, and the National Fish and Wildlife Laboratory, U.S. Fish and Wildlife Service.

LITERATURE CITED

BELOPOL'SKII, L. O.
1939. On the migrations and ecology of reproduction of the Pacific walrus (*Odobaenus rosmarus divergens* Illiger). Zool. Zh. 18:762-774.

BROOKS, J. W.
1954. A contribution to the life history and ecology of the Pacific walrus. M.S. Thesis, University of Alaska, Fairbanks, 103 p.

COLLINS, G.
1940. Habits of the Pacific walrus (*Odobenus divergens*). J. Mammal. 21:138-144.

ESTES, J. A., and J. R. GILBERT.
1978. Evaluation of an aerial survey of Pacific walruses (*Odobenus rosmarus divergens*). J. Fish. Res. Board Can. 35:1130-1140.
FAY, F. H.
1955. The Pacific walrus: spatial ecology, life history, and population. Ph.D. Thesis, Univ. British Columbia, Vancouver, B.C., Canada, 171 p.
1957. History and present status of the Pacific walrus population. Trans. North Am. Wildl. Conf. 22:431-443.
FEDOSEEV, G. A.
1962. On the status of stocks and distribution of the Pacific walrus. Zool. Zh. 41:1083-1089.
GOL'TSEV, V. N.
1968. Dynamics of coastal herds of walruses in connection with their distribution and numbers. *In* V. A. Arsen'ev and K. I. Panin (editors), Pinnipeds of the northern part of the Pacific Ocean, p. 205-215. Pischevaya Promyshlennost', Moscow.
KRYLOV, V. I.
1962. Rates of reproduction of the Pacific walrus. Zool. Zh. 41:116-120.
1968. Present condition of the Pacific walrus stocks and prospects of their rational exploitation. *In* V. A. Arsen'ev and K. I. Panin (editors), Pinnipeds of the northern part of the Pacific Ocean, p. 189-204. Pischevaya Promyshlennost', Moscow.
NIKULIN, P. G.
1947. Biological characteristics of the shore herds of the walrus on the Chukchi Peninsula. Izv. TINRO 25:226-228.
TOMILIN, A. G., and A. A. KIBAL'CHICH.
1975. Walruses of the Wrangell Island region. Zool. Zh. 54:266-272.

An Analysis of a Hypothetical Population of Walruses

DOUGLAS P. DeMASTER[1]

ABSTRACT

A series of computer simulations of the Pacific walrus population, using a variable Leslie model, were conducted primarily to test the hypothesis that the population increased from about 70,000 in 1955 to about 200,000 in 1975 and, secondarily, to evaluate the reliability of the data available on adult survival rates. Published estimates of the population size, the sex ratio of adults, age at sexual maturity, average reproductive rate, adult mortality, and size and sex/age composition of the annual harvests were incorporated into the model. The results suggested that, either the estimates of size of the 1955 population were too low, or that the survival rates of adults were significantly higher than believed. They suggested further that an increase to 200,000 in 20 yr would have been possible, if the initial population in 1955 had been made up of about 94,000 to 98,000 animals, the sex ratio of adults was 1 male:3 females, and the adult survival was 0.96, with nonlinear density dependence. Such an increase would have been impossible with linear density dependent functions, smaller initial population size, or lower adult survival rates. The maximum sustained yield (MSY) of the hypothetical population, assuming continuation of the current harvest composition at 3 males:1 female, would be between 3 and 5% and should be available when the population is between 59 and 91% of the carrying capacity (K), assuming environmental stability. The maximum net productivity (MNP) of this hypothetical population was estimated to be attained at 50 to 84% of K.

РЕЗЮМЕ

Моделирование на счетно-решающем устройстве было произведено с помощью «переменной модели Лесли», главным образом, чтобы проверить гипотезу об увеличении численности тихоокеанского моржа приблизительно с 70,000 в 1955 г. до 200,000 голов в 1975 г., а также оценить надежность имеющихся данных о способности выживания взрослых зверей. Опубликованные данные по оценке величины популяции, половому соотношению взрослых, возрасту полового созревания, среднему темпу воспроизводства, смертности взрослых, возрастному составу и ежегодной добычи использовались в модели. Результаты дают основание предполагать, что величина популяции в 1955 г. была слишком низкой или темп выживания взрослых был гораздо выше, чем это считалось ранее. Кроме того, результаты позволяют предполагать, что увеличение до 200,000 голов в течение 20 лет было бы возможным, если популяция в 1955 г. составляла 94 - 98,000 голов, половое соотношение взрослых 1 самец: 3 самки и выживание взрослых - 96% с нелинейной плотностью зависимости. Такое увеличение было бы невозможным с линейной плотностью зависимости, меньшей первоначальной величной популяции, или низким выживанием взрослых. Максимальная ежегодная добыча гипотетической популяции, при сохранении в добыче соотношения 1 самка: 3 самца, будет составлять 3 - 5%. Такой уровень добычи возможен, если при максимальной плотности саморегулирующейся популяции [K = 59 - 91%] и стабильности экосистемы. Считаем, что максимальное чистое производство этого гипотетического населения достигается при 50 - 84% K.

По оценке автора максимальная чистая продуктивность данной гипотетической популяции может быть достигнута при K = 50 - 84%.

INTRODUCTION

In the late 1950's, the size of the Pacific walrus, *Odobenus rosmarus divergens*, population was considered to have been between 40,000 and 70,000 animals (Fay 1957; Kenyon 1960;[2] Fedoseev 1962). Nevertheless, Kenyon (footnote 2) felt that the actual population size in the late 1950's may have been higher than 70,000. Estes (1976),[3] Estes and Gilbert (1978), and Estes and Gol'tsev (1984) supported Kenyon's judgement with evidence that Fay and Fedoseev had underestimated the number of walruses in the American sector of the Chukchi Sea. More recent estimates of the Pacific walrus population have placed it at 140,000 to 200,000 (Estes and Gol'tsev 1984) and 168,000 to 250,000 individuals (Krogman et al. 1978[4]). Estes and Gilbert (1978) concluded that estimates produced from limited aerial surveys should not be considered reliable.

Perhaps the best quantitative information available concerning the Pacific walrus population is contained in the American and Soviet harvest data from 1959 to 1975 (Harbo 1961;[5] Burns 1965[6]

[1]National Fish and Wildlife Laboratories, U.S. Fish and Wildlife Service, Anchorage, Alaska; present address: Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, USA.

[2]Kenyon, K. W. 1960. Aerial surveys of marine mammals in the Bering Sea, 23 February to 2 March 1960 and 25-28 April 1960. Unpubl. rep., 39 p. U.S. Bur. Sport Fish. Wildl., Seattle, WA 98115.

[3]Estes, J. A. 1976. The reliability of aerial surveys to estimate population abundance of marine mammals. Consideration from a survey of Pacific walrus. Scientific Consultants on Marine Mammals, Bergen, Norway. 31 August-September 1976. [FAO] Advis. Comm. Mar. Resour. Res. ACMRR/80, 13 p.

[4]Krogman, B. D., H. W. Braham, R. M. Sonntag, and R. G. Punsly. 1978. Early spring distribution, density, and abundance of the Pacific walrus (*Odobenus rosmarus*) in 1976. Final report R.U. 14, 47 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

[5]Harbo, S. J., Jr. 1961. Walrus harvest and utilization. Annual project segment report, Federal Aid in Wildlife Restoration. Alaska Dep. Fish Game, Juneau, 25 p.

[6]Burns, J. J. 1965. The walrus in Alaska, its ecology and management. Alaska Dep. Fish Game, Juneau, 48 p.

and unpubl. data; Krylov 1968; F. H. Fay[7]). These data include the retrieved kill and estimated losses from wounding and sinking; for the American harvest, they also include the sex ratio of adults and the number of calves taken. Studies of the reproductive organs from the harvested animals have produced estimates of age-specific rates of fecundity (Fay 1960;[8] Burns footnote 6; Krylov 1968), but these estimates generally have not been accepted due to suspected sampling bias in the harvests and in the assumptions of the estimation process.

To date, then, "relatively" reliable information exists on the size and sex/age composition of the Alaskan walrus harvests from 1955 to 1975, and on the age-specific rates of reproduction. Only the total harvests are known from the Soviet side. The estimates of population size in 1955 to 1975 are questionable, and the estimated rates of natural mortality appear to be unreliable. Nevertheless, these were the best figures available and of sufficient quality for use in a preliminary computer model of the Pacific walrus population.

The primary purpose of integrating the existing estimates of population parameters into the format of a computer model was to test the hypothesis that the Pacific walrus population could have increased in size from 70,000 to 200,000 animals in the 20 yr from 1955 to 1975. Such a model can be used also to estimate unknown parameters, when all others are fixed, and to assess the reliability of any that are in question. In addition, the interrelationships between the various parameters can be examined, and a better understanding can be gained of the relative importance of each to the population.

METHODS

The population model used in this instance was a modification of Leslie's (1945) model, as described by DeMaster (1981); similar models were described by Fowler and Smith (1973) and by Fowler and Barmore (1977).[9] The model assumes that the influence of density dependence on the life history parameters will be within the range of the following two types of functions:

$$Pi = A - c\,N_x \qquad \text{(linear)}$$

$$Pi = A\,(1-\exp\,[-b\,(k-N_x)]) \qquad \text{(nonlinear)}$$

where Pi = annual survival of the ith age class
A = maximum annual survivorship
N_x = number of females 4 yr old and older
k = maximum number of females 4 yr old and older
b = constant associated with the shape of the curve
c = constant associated with the slope of the curve.

The initial values for the projection matrix (Tables 1, 2) were derived from the American and Soviet data. Only the female segment of the population was incorporated into the model; the sex ratio was assumed to be constant at 1 male:3 females (Fay 1982). The initial population vector was calculated by solving the following equation for N_0, the number of female calves in the initial population:

Table 1.—Parameters used in the population models, where m_x is the age specific reproductive rate, and p_x is the age specific survivorship.

Age	m_x	p_x	Age	m_x	p_x
0	0	0.94	20	0.22	0.96
1	0	.90	21	.22	.96
2	0	.94	22	.22	.96
3	0	.96	23	.22	.96
4	0	[1].96	24	.22	.96
5	0.10	.96	25	.15	.96
6	.12	.96	26	.15	.96
7	.17	.96	27	.15	.96
8	.22	.96	28	.15	.96
9	.22	.96	29	.15	.96
10	.22	.96	30	.15	.96
11	.22	.96	31	.15	.96
12	.22	.96	32	.15	.96
13	.22	.96	33	.15	.96
14	.22	.96	34	.15	.96
15	.22	.96	35	.15	.96
16	.22	.96	36	.15	.96
17	.22	.96	37	.15	.96
18	.22	.96	38	.15	.96
19	.22	.96	39	.15	.96

[1]Survival from age 4 and older assumed to be density dependent. All other parameters are assumed constant.

Table 2.—Assumed parameters for estimation of adult survival necessary for the population to increase from 70,000 to 200,000 in 20 yr.

Parameter	1955	1975
Female population	52,500	150,000
Total population	70,000	200,000
Sex ratio	1♂:3♀	1♂:3♀
Female kill	1,675	1,675
Total kill	6,700	6,700
Sex ratio of kill	1♀:3♂	1♀:3♂

$$P = N_0 + .94\,N_0 + (.94)(.90)N_0 + (.94)^2(.90)N_0 + \sum_{x=1}^{36}(.94)^2(.90)(.96)^x$$

where $P = 52{,}500$, the number of females in a population of 70,000 walruses. Subsequent age classes were calculated by using the age-specific survival rates from Table 1.

The number of females 4 yr old and older (k) in the maximal population of about 200,000 walruses (Fay 1957) was assumed to be 150,000. The constant b was arbitrarily set at 0.002, which represents a relatively rapid change in the shape of the nonlinear function (Eberhardt and Siniff 1977). The constant c was set at 0.0000007, which was calculated directly from the nonlinear model as the slope between the two points described by the survivorship and the population at equilibrium, given an initial survivorship of 0.96 at a population level of 0 (DeMaster 1981). In this way, the simulations with linear and with nonlinear density dependence had the same equilibrium population.

The population model assumed that only animals 4 yr old and older were harvested. The harvest of a particular age class was weighted in proportion to the frequency of occurrence of that age class in the harvest data. Compensatory and additive harvests were represented by the following equations (DeMaster 1981):

[7]F. H. Fay, Associate Professor, Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, pers. commun. October 1979.

[8]Fay, F. H. 1960. Investigations of the Pacific walrus. Terminal report, Project 26. Arctic Institute of North America, Montreal, Canada, 72 p.

[9]Fowler, C. W., and W. J. Barmore. 1977. A population model of the northern Yellowstone elk herd. *In* R. M. Linn (editor), Proceedings First Conference on Scientific Research in the National Parks, New Orleans, Louisiana, November 9-12 1976. Vol. 1, p. 427-434.

harvest mortality additive:

$$X\ (i+1) = L[X\ (i) - H\ (i)],$$

harvest mortality compensated for:

$$X\ (i+1) = L[X\ (i) - H\ (i)],$$

where $X\ (i)$ = the population vector at time i
L = the projection matrix
$H\ (i)$ = the harvest vector.

Using this model, a series of simulations was computed in which the maximum annual survivorship (A) was increased in each simulation until the population model produced the desired final size. The total kill of females was assumed to be constant over the 20-yr period. The average kill was derived from known harvest data.

RESULTS

The hypothetical population, given a nonlinear density dependent function, increased from 70,000 to 200,000 in 20 yr only when A, the annual survivorship, was set to equal 0.99. This value of A was necessary whether or not the harvest mortality was compensatory. The simulated population, given a linear density dependent function, could not increase from 70,000 to 200,000 in 20 yr, even when A was set at 1.00.

Because the natural rate of adult survival probably could not have been as high as 0.99 to 1.00, one must assume that some other component of the model is incorrect. For the reasons given by Estes and Gilbert (1978), the most questionable component is the initial size of the population. Given the entries for the projection matrix from Tables 1 and 2 (excluding initial population size), nonlinear density dependence, and a harvest mortality that was additive, the initial population of females would have had to have been 73,828 (total population 97,828) to have produced the hypothetical final population of 200,000 in 20 yr. If the harvest mortality was assumed not to be additive, an initial population of 70,645 females (total population 94,194) would have been necessary for the increase to 200,000. If the form of the density dependent function was assumed to be linear, initial populations even of these sizes could not have reached 200,000 in 20 yr, given an adult female harvest of 1,675/yr.

In the United States, the Marine Mammal Protection Act of 1972 (MMPA) dictates that marine mammals should be managed at the level of "optimum sustainable population" (OSP). The concept of OSP is interpreted to mean that the population should remain between an upper level imposed by environmental constraints (commonly called K) and a lower level at which the population would produce the greatest annual increment (maximum net productivity = MNP) if the population were not being harvested. To estimate this lower level directly from a population that is being harvested is impossible, but it can be estimated through modeling. Given the age specific rates of births and deaths in Table 1 and the nonlinear density dependent function previously described, the MNP of the simulated population would occur at 84% of K, the equilibrium population (Table 3). For simulations with linear density dependence, the MNP would occur at 50% of K. If we assume that the real MNP is within the range of these two forms of density dependence, the lowest level of the population that would be acceptable under the MMPA would be between 50 and 84% of K.

Current information on the Pacific walrus population suggests that it has increased dramatically since 1955. Within the guidelines of the MMPA, the population could conceivably be managed somewhere between K and the MNP levels. As a starting point, the maximum sustainable yield (MSY) of a specific segment of the population can be estimated, but only if various age and sex specific life history parameters are known. In addition, how these parameters respond to changes in density must be known. Even then, the estimated MSY is only reliable if the environment is relatively constant. To estimate the MSY of adult female walruses, a series of simulations were computed, in which the harvest was continually increased, until the population no longer could sustain it (DeMaster 1981). Using the life history parameters of Table 1 and a nonlinear form of density dependence, the MSY of adult females (females 4 yr and older) would be 5.1% of the total population of females, and would occur at 91% of K (Table 3). If the density dependent function was assumed to be linear, the MSY of adult females would be 2.3%, and would occur at 59% of K. Obviously, we do not know the proper form of the density dependent function, but these results suggest that an adult female harvest of 2 to 5% could be sustained, and presumably would result in the population reaching an equilibrium when it was between 59 and 91% of K.

Table 3.—Comparative dynamic characters of walrus population models with linear and nonlinear density dependence.

Character	Density dependence	
	Linear	Nonlinear
Maximum net productivity (MNP)	50% of K	84% of K
MSY (no compensation)	2,100 adult females	6,800 adult females
Population at MSY_{nc}	59% of K	86% of K
MSY (compensation)	2,200 adult females	7,400 adult females
Population at MSY_c	59% of K	91% of K

DISCUSSION

The exact details of the recovery of the Pacific walrus population are not known, but at least a partial recovery has taken place (Burns footnote 6; Fay footnote 8; Estes and Gilbert 1978; Estes and Gol'tsev 1984). This recovery has occurred in spite of a continual harvest of adults. The average growth rate necessary for a population to double in 20 yr is 1.035, and to triple in 20 yr is 1.056. Such rates of growth are common for many species of marine mammals (Eberhardt and Siniff 1977), but seem somewhat improbable in this instance, considering the low productivity and ongoing harvest of Pacific walruses.

The purpose of this paper was to produce a model that would incorporate the existing data and shed some light on the reliability of the estimate of population size in 1955 and the estimated rate of annual mortality. The results from the various simulations suggest that, either the natural rate of adult mortality is extremely low relative to other pinnipeds (Eberhardt and Siniff 1977), or that the population estimate for 1955 was too low.

The model described in this paper was based on numerous assumptions for which substantive data are few and, in some cases, questionable. In all of the simulations, I assumed that the sex ratio of the adult population remained constant at 1 male:3 females, based on Fay's (1982) derivations from shipboard visual and aerial photographic surveys of the Pacific walrus population. Further information on herd composition and how it varies throughout the year is needed for improvement of the estimate of adult sex ratio. Simulations in which the sex ratio is assumed to be 1:2 and 1:1 also should be computed. The effect of these would be to increase the difference between the estimated and required population in 1955, given the

life history values of Table 1. Increasing this difference will only strengthen the argument that either the 1955 population estimate was too low or that estimates of adult survival were too low. Second, I have assumed that the environment of the walrus remained relatively constant. Although human perturbation (other than hunting) probably has been minimal over the past 20 yr, natural perturbations may have occurred and not been recognized.

In all of the simulations where a harvest took place, I assumed that the sex ratio of the harvest was 3 males:1 female, and that a constant number was taken each year. Data concerning the sex ratio of the harvest supports a 1:3 ratio (Burns footnote 6; Fay footnote 8), but the numbers taken were not constant; rather, they declined from about 9,000 in 1955 to about 3,000 in 1969, and have been rising slowly since then to about 7,000. The effects of these changes on the population probably were insignificant, if the initial harvests were low enough to allow the population to increase (which, apparently, it did).

Data on the kinds of density dependent factors influencing this population were not available at this writing. Simulations which incorporate density dependent reproduction or calf survival should be computed.

Evidence from Weddell seals, *Leptonychotes weddelli*, suggests that reproduction may be relatively unaffected by changes in density, because the time of reproduction does not coincide with the seasonal onset of poor feeding conditions (DeMaster 1981), and this may be the case for walruses as well. One could assume that all independent walruses will be affected equally by food shortages, and that younger individuals will not be more disadvantaged than the older ones in obtaining food. The advantages usually invoked for older pinnipeds, such as greater experience with the area, better diving capabilities, and outright dominance, may not apply under conditions where all feeding is done in relatively shallow waters, the distribution of the ice dictates which areas can be utilized, and a major portion of the adult males may not be feeding in the same areas where the subadults and adult females feed. Obviously more information is needed on these points.

Throughout this paper, a distinction has been made between natural mortality and mortality due to harvests. One problem that arises in estimating mortality rates from age composition of the harvest is that mortality from both sources is combined. Furthermore, estimates of mortality derived from samples of populations that are growing will be biased upward (Payne 1977). Burns (footnote 6) suggested that adult male mortality was about 13%/yr, based on the age fecundity from the harvest. If the Pacific walrus population was growing at about 5%/yr, the estimate of survival from age composition will be negatively biased (Payne 1977). When corrected as:

$$S = e^{(\ln .87 + \ln 1.050)} = .91$$

where S = annual survivorship, the better estimate for adult male mortality would be 9%/yr. Again, this includes both natural and hunting mortality. If the Pacific walrus is polygynous (Fay et al. 1984), and the harvest of males is greater than that of females, the rate of natural mortality for adult females should be less than the total mortality for adult males, rather than greater as indicated by Burns (footnote 6). Therefore, the male mortality rate of 13% (Burns footnote 6) should exceed the maximum for adult females, the actual rate probably being much lower.

All of the simulations in which the population increased as rapidly as hypothesized (3 to 5%/yr) required that natural adult survivorship be above 95%, given the known level of harvest. The model suggests that the Pacific walrus population was theoretically capable of increasing from 70,000 to 200,000 in 20 yr, but to have done so, the sex ratio of the population would have had to have been strongly weighted to females. Information on the current sexual composition of the population would, therefore, be extremely useful for better understanding of the population dynamics of this species.

Finally, the model suggests that the MNP of a population varies considerably with the type of density dependence that is operative. This has been demonstrated also for MSY values (DeMaster 1981). MNP values for marine mammals commonly are assumed to lie between 50 and 60% of K. More realistic estimates of MNP will require information on the age at which density related changes take place in life history parameters, and on the form of the relationship between life history parameters and density of the population.

ACKNOWLEDGMENTS

The author wishes to thank L. L. Eberhardt and C. W. Fowler for reading and commenting on an earlier draft of this paper, and J. J. Burns and F. H. Fay for providing unpublished data on population parameters and composition of recent walrus harvests.

LITERATURE CITED

DeMASTER, D. P.
1981. Incorporation of density dependence and harvest into a general population model for seals. *In* C. W. Fowler and T. D. Smith (editors), Dynamics of large mammal populations, p. 389-401. Wiley-Interscience, N.Y.

EBERHARDT, L. L., and D. B. SINIFF.
1977. Population dynamics and marine mammal management policies. J. Fish. Res. Board Can. 34:183-190.

ESTES, J. A., and J. R. GILBERT.
1978. Evaluation of an aerial survey of Pacific walruses (*Odobenus rosmarus divergens*). J. Fish. Res. Board Can. 35:1130-1140.

ESTES, J. A., and V. N. GOL'TSEV.
1984. Abundance and distribution of the Pacific walrus, *Odobenus rosmarus divergens*: Results of the first Soviet-American joint aerial survey, autumn 1975. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:67-76.

FAY, F. H.
1957. History and present status of the Pacific walrus population. Trans. North Am. Wildl. Nat. Resour. Conf. 22:431-443.
1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North Am. Fauna 74, 279 p. U.S. Fish Wildl. Serv., Washington, D.C.

FAY, F. H., G. C. RAY, and A. A. KIBAL'CHICH.
1984. Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:89-99.

FEDOSEEV, G. A.
1962. On the status of the stocks and the distribution of the Pacific walrus. Zool. Zh. 41:1083-1089.

FOWLER, C. W., and T. SMITH.
1973. Characterizing stable populations: an application to the African elephant population. J. Wildl. Manage. 37:513-523.

KRYLOV, V. I.
1968. Present condition of Pacific walrus stocks and prospects of their rational exploitation. *In* V. A. Arsen'ev and K. I. Panin (editors), Pinnipeds of the northern part of the Pacific Ocean, p. 189-204. Pischevaya Promyshlennost', Moscow.

LESLIE, P. H.
1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

PAYNE, M. R.
1977. Growth of a fur seal population. Philos. Trans. R. Soc. Lond. 279:67-79.

Foods of the Pacific Walrus in Winter and Spring in the Bering Sea

FRANCIS H. FAY,[1] YURI A. BUKHTIYAROV,[2] SAMUEL W. STOKER,[1] and LARRY M. SHULTS[1]

ABSTRACT

Part of the information required for effective multispecies management of the marine resources of the Bering Sea is a documentation of the feeding habits of the pinnipeds residing there. In this report, new data on the foods of walruses in their wintering areas and along a major spring migration route through Bering Strait are summarized. These data were acquired during several research cruises and shore-based studies from 1970 to 1976. In general, the findings from those studies indicate a primary reliance of the walruses in all areas on a few genera of bivalve mollusks, namely *Serripes*, *Mya*, and *Hiatella*, with significant but lesser reliance on other bivalves, priapulids, polychaetes, snails, molting brachyuran crabs, and holothureans. In areas where both male and female walruses were sampled, the adult males tended to eat organisms which were about six times as large as those taken by the adult females, suggesting that the sexes are selectively partitioning food supplies in those areas. The need for further quantitative information on the feeding habits of the walruses in their primary wintering areas, and on the benthic faunas of those areas, is emphasized.

РЕЗЮМЕ

Для эффективного управления комплексом морских ресурсов Берингова моря нужны данные о питании ластоногих, обитающих в этом регионе. В докладе излагаются новые данные о питании моржей в зимних районах обитания и на основных путях весеней миграции. Материал получен во время нескольких научных рейсов и береговых исследований с 1970 до 1976 г. В основном, полученные сведения указывают, что моржи во всех районах используют небольшое число родов двустворчатых моллюсков, конкретно *Serripes, Mya, Hiatella* и в меньшей степени приапулид, многощетинковых червей, брюхоногих моллюсков, линяющих десятиногих крабов, голотурий. В районах, из которых получены самцы и самки моржей, взрослые самцы проявляли тенденцию питаться организмами в шесть раз большими по величине, чем организмы, которыми питались взрослые самки. Этот факт даёт основание предполагать, что оба пола селективно используют пищевые запасы в этих районах.

Подчёркивается необходимость продолжения сборов по питанию моржей в основных районах зимнего обитания и изучения бентосной фауны в этих районах.

INTRODUCTION

To the common knowledge that walruses, *Odobenus rosmarus* (L.), feed principally on bivalve mollusks, Chapskii (1936), Nikulin (1941), Vibe (1950), Brooks (1954), Krylov (1971), and Fay et al. (1977)[3] have contributed a substantial amount of specific information on the kinds and quantities of prey that walruses eat. As a whole, those findings indicated that the quality of the walrus' diet varies seasonally and geographically, and that it is made up of more than 60 different kinds of benthic organisms.

The need for further quantitative information on the feeding habits of walruses and other pinnipeds of the Bering Sea has become increasingly apparent in recent years. In order to facilitate multiple resource management, detailed knowledge of the interrelationships and interdependencies among the major components of the system is required. For a sea of its size, the Bering Sea is one of the richest in the world, as shown by its highly productive fisheries and large marine mammal populations.

The information presented in this report is a contribution to the data base concerning the food web of the Bering Sea. It consists of new qualitative and quantitative data on the feeding habits of a major component of that system, the Pacific walrus population. Walruses are dependent on the benthic resources of the region, principally during the winter and spring of each year. This information was acquired by American and Soviet biologists during the course of five scientific expeditions: 1) The oceanographic cruise of the US Coast Guard Cutter (CGC) *Northwind* in the northern and eastern Bering Sea in January-February 1970; 2) the marine mammal research cruise of the CGC *Glacier* in the north-central Bering Sea in March-April 1971; 3) the oceanographic-marine mammal cruise of the CGC *Burton Island* in the north-central Bering Sea in February-March 1972; 4) the Alaskan walrus harvest monitoring program in northern Bering Sea-Bering Strait during April-June 1974-76; and 5) the joint Soviet-American marine mammal research cruise of the ZRS *Zagoriany* in the southeastern Bering Sea in March-May 1976. The largest samples were obtained during the last two of those endeavors.

METHODS

The kinds and quantities of prey eaten by walruses were determined mainly from examination of stomach contents of animals taken at sea. Some of those specimens were obtained for scientific

[1]Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, USA.

[2]Magadan Branch, Pacific Research Institute of Fisheries and Oceanography (MoTINRO), Nagaevskaya 51, Magadan 685013, USSR.

[3]Fay, F. H., H. M. Feder, and S. W. Stoker. 1977. An estimation of the impact of the Pacific walrus population on its food resources in the Bering Sea. U.S. Mar. Mammal Comm., Wash., D.C., 38 p.

purposes, during the *Northwind* and *Zagoriany* expeditions; the rest were taken by Alaskan Eskimos during the spring walrus harvests of 1974-76. The localities in which the samples were obtained are shown in Figure 1.

For each animal, the date, location, sex, and age were recorded. Age was determined from counts of cementum layers in thin, longitudinal sections of the postcanine teeth, as described by Mansfield (1958) and Krylov (1965).

Whenever possible, the entire contents of the stomach were examined in detail. All intact prey were sorted into taxonomic groups, each group weighed to the nearest whole gram, and the number of individuals counted. Since the specific gravity of the food items was essentially the same as that of water, their weight in grams was tantamount to volume in milliliters. Unless stated otherwise, composition of stomach contents is expressed as percent by volume.

The remaining particulate organic matter was separated from the free fluids by centrifugation and weighed to the nearest gram. Large inorganic solids (stones and gravel) were removed at the time of sorting; the finer particles were separated by dilution and decantation. The total inorganic solids were air-dried, weighed, and their volume determined by water displacement.

In a few field situations, where such procedures were not feasible, the percentage composition of the ingesta by major taxa was estimated at the time of collection, and a small sample of each taxon was preserved in 10% Formalin[4] for subsequent identification and reference.

On a few occasions, individual food items were retrieved from the surface of the ice adjacent to breathing holes used by walruses. Walruses often bring such items to the surface in their mouth and occasionally drop them on the ice. We presume that this is unintentional, since the same kinds of items occur commonly in the stomach contents. On a few occasions, we also collected and analyzed samples of feces found on the ice where walruses had lain. Since many of the organisms eaten by walruses have indigestible skeletal parts which are diagnostic of the genus, fecal samples are of some value in assessing the frequency of occurrence of those genera in the diet.

RESULTS

Cruise of the CGC *Northwind*, January-February 1970

Four walruses were collected, three of which had food in the

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

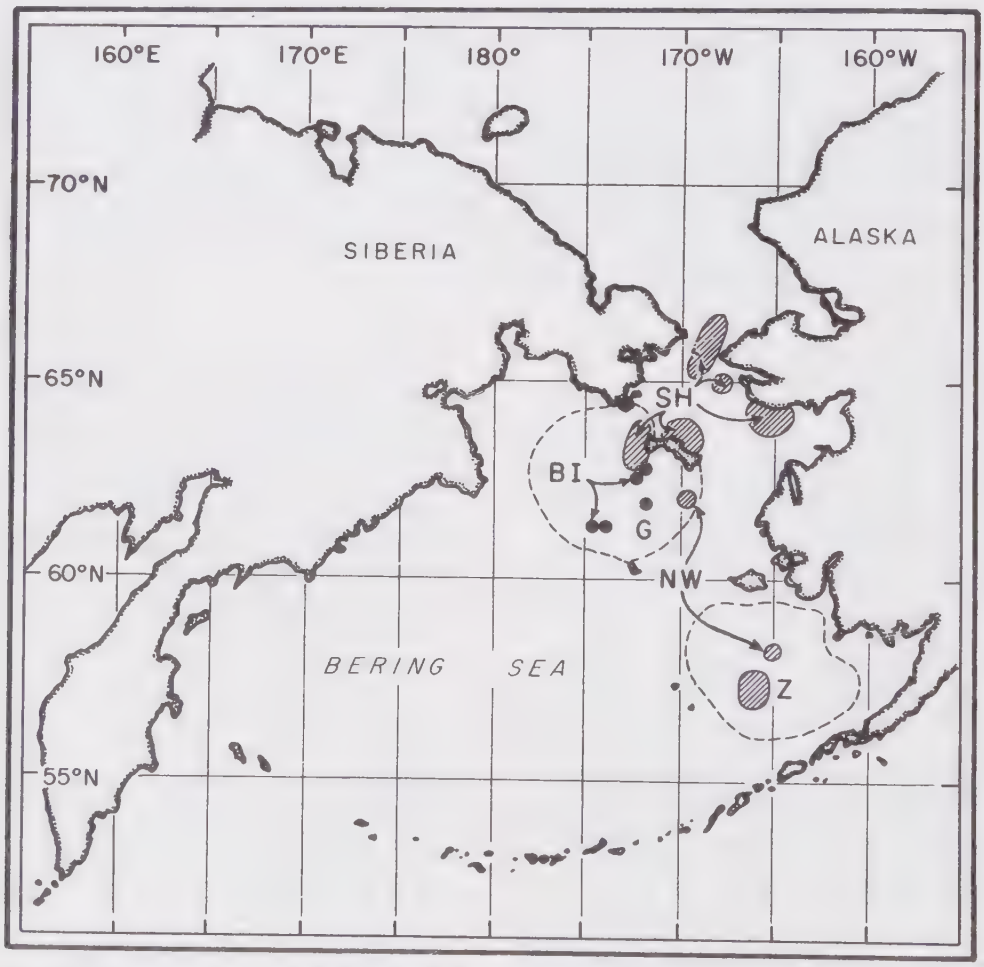


Figure 1.—Chart of the eastern Bering Sea, showing locations in which samples of stomach contents (cross-hatched) and feces (dashes) of walruses were collected. BI = *Burton Island* expedition, March 1972; G = *Glacier* expedition, April 1971; NW = *Northwind* expedition, January-February 1970; SH = spring harvest areas, 1974-76; Z = *Zagoriany* expedition, March-April 1976. Dash lines indicate approximate limits of wintering areas, as currently known (after Fay 1982).

stomach. The first two were taken about 215 km south of Etolin Strait in water 45 m deep. One of these, an adult male, contained 10.9 kg of the cockle *Serripes groenlandicus*; no other kinds of prey were represented. The other, a subadult male, contained 3.71 kg of ingesta, made up of about 60% whelks of the genera *Neptunea* and *Buccinum*, 25% *S. groenlandicus*, 5% whole tunicates (cf. *Tethyum* sp.), and 10% stones and gravel. The third specimen with food in its stomach was an adult female taken about 55 km south of the southeastern cape of St. Lawrence Island, where the water was 33 m deep. This animal contained about 2.04 kg of ingesta made up of 53% tunicates of the species *Pelonaia corrugata*, 25% bavalves represented about equally by *Mya* spp. and *S. groenlandicus*, 10% whelks and other snails of the genera *Buccinum*, *Natica*, and *Polinices*, 2% amphipods and crangonid shrimps, 1% *Echiurus echiurus*, and 9% stones and gravel.

Cruise of the CGC *Burton Island*, February-March 1972

Four specimens were collected during this cruise, all of which had empty stomachs. We found several items on the ice alongside breathing holes used by walruses, approximately 260 km southwest of the western end of St. Lawrence Island over water 82 m deep. Most of these were remains of the bivalve *Macoma calcarea*, one of the most common mollusks in that area (Stoker 1978); one was *Musculus niger*. In addition, we analyzed two samples of walrus feces collected from the ice in that location (samples I, II, Table 1). The dominant remains in each were operculae of snails of the genera *Natica* and *Polinices*, and exoskeletons of the brachyuran crab *Chionoecetes* sp. Two fecal samples from another locality, 65 km southwest of the island over waters 60 m deep, were similar in composition but included also several periostracal sheaths of siphons, probably from bivalves of the genus *Mya*, and tests of *Priapulus caudatus* (samples III, IV, Table 1).

Cruise of the CGC *Glacier*, March-April 1971

One specimen with empty stomach was collected during this cruise. However, remains of several food items were found on the ice near breathing holes used by a large herd of walruses about 165 km south of the western end of St. Lawrence Island over water 60 m deep. These were as follows: *Musculus niger* — shells of four individuals from which most of the fleshy parts had been removed; *Neptunea heros* — one intact individual; *Pagurus trigonochierus* — one intact individual in a shell of *N. heros*; and four fragments of egg cases from an unidentified gastropod mollusk. A sample of feces collected from the ice where some of the walruses had lain contained remains of 47 individual prey (sample V, Table 1). The dominant taxa were the mollusks *Nucula tenuis*, *Neptunea* sp., and *Polinices* sp.

Cruise of the ZRS *Zagoriany*, March-April 1976

Of 158 walruses collected during this cruise, 21 had food in their stomachs. These were all taken in southeastern Bering Sea, within an area bounded by lat. 56°43′ to 57°30′N and long. 165°10′ to 166°31′W. The greatest amount in one stomach was 29 kg; the weight of the ingesta relative to the total body weight of the animals ranged from 2.1 to 2.7%. Seven taxa were identified in the stomach contents (Table 2). Brachyuran crabs of the genus *Chionoecetes* and whelks of the genera *Neptunea* and *Buccinum* occurred more frequently than any other kinds of prey, but were of secondary importance in volume compared with the bivalve mollusks, especially the cockle *S. groenlandicus*. Nearly all of the cockle feet were of uniformly small size (mostly 5 to 6 cm long), but nearly all of the whelks were unusually large relative to those found in walrus stomachs in other areas. All of the brachyuran crabs were in the soft-shelled (molting) stage. Several animals observed immediately to the southwest of the collection area appeared to be feeding in

Table 1.—Comparative numbers of prey (represented by undigested parts) in fecal samples from walruses at five locations in the north-central Bering Sea, during late winter to early spring.

	Sample no. and location[1]						
	I	II	III	IV	V	Overall	
Lat.	61°27′N	61°26′N	62°55′N	62°47′N	61°52′N		
Prey type Long.	174°24′W	174°27′W	172°11′W	172°28′W	171°45′W	No.	%
Worms							
Priapulus	—	—	—	18	2	20	8
Echiurus	—	1	1	1	—	3	1
Bivalves							
Mya	—	—	10	—	—	10	4
Nucula	—	1	1	—	13	15	6
Gastropods							
Neptunea	1	—	1	2	14	18	7
Buccinum	5	4	2	—	3	14	6
Natica	10	16	7	12	—	45	18
Polinices	21	12	9	15	12	69	28
Margarites	—	—	—	1	—	1	tr
Crabs							
Chionoecetes	8	7	1	4	1	21	9
Shrimps							
Argis	—	1	2	4	—	7	3
Amphipods							
Maera	—	—	4	—	—	4	2
Anonyx	—	—	—	4	—	4	2
Tunicates							
Pelonaia	—	2	4	2	—	8	3
Tethyum	—	—	1	4	2	7	3
Totals	45	44	43	67	47	246	100

[1]Samples I to IV from *Burton Island* expedition, March 1972; sample V from *Glacier* expedition, April 1971.

Table 2.—Frequency of occurrence and relative abundance of prey in stomachs of 21 walruses from the *Zagoriany* expedition, southeastern Bering Sea, March-April 1976.

Prey type	Frequency in stomachs (%)	Maximal number of individuals per stomach
Serripes groenlandicus	33	2,881
Mya	24	79
Bivalve, unidentified	24	1,360
Neptunid snails	62	342
Hyas coarctatus	5	1
Chionoecetes sp.	62	969
Tunicates, unidentified	5	7

waters 80 to 90 m in depth; in the collection area itself, depths ranged from about 65 to 80 m. We observed one adult male for nearly 2 h while it apparently was feeding in 79 m of water. During that time, it dove 12 times, each dive ranging in length from 2 min, 10 s to 10 min, 2 s (mean, 7 min, 47 s); it remained at the surface between dives for 31 s to 2 min, 6 s (mean, 1 min, 34 s). Feces on the ice nearby, where several walruses had lain, contained abundant remains of gastropods of the genera *Neptunea*, *Buccinum*, and *Polinices*, and of crabs of the genus *Chionoecetes*. The presence in the feces of several diphyllobothriid cestodes suggested that some fishes also had been eaten.

Harvest Monitoring Program, April-June 1974-76

Stomachs containing ingesta were acquired from five localities in the northern Bering Sea-Bering Strait region (Fig. 1). Results of the analyses of these samples are presented in detail in Tables 3-7.

West of St. Lawrence Island.—Stomachs from 10 males and 3 females contained from < 1 to more than 14 kg of ingesta (mean, 5.75 kg), 98% of which, by volume, was organic matter. Nearly 90% of the identifiable organic materials were parts of mollusks, the majority of which were bivalves of the genera *Hiatella* and *Mya* (Table 3). These two genera made up 87% of the total number of prey and 54% of the total volume of ingesta.

North of St. Lawrence Island.—Stomachs of 13 males and 1 female contained from 0.3 to more than 22 kg of ingesta (mean, 8.26 kg), 99% of which were organic and the remainder inorganic solids. Nearly all (97%) of the identifiable materials were parts of mollusks, of which two genera of bivalves (*Serripes* and *Mya*) made up 87% of the number and at least 80% of the volume of organic matter in the stomachs (Table 4).

South of Nome.—Stomachs from seven males contained from 0.4 to 7.9 kg each (mean, 3.6 kg), 99.8% of which was organic matter. Nearly all of the identifiable prey were mollusks, one of which (*Serripes*) made up 98% of the number of individuals and 73% of the total volume of ingesta (Table 5). The feet of these *Serripes* were very small (5-6 cm long, 1-2 g each), comparable with those found in the *Zagoriany* sample from southeastern Bering Sea.

King Island.—Stomach contents were obtained from an adult female and a juvenile male. The volume of ingesta was 3.8 kg in the female and 14.7 kg in the male. Nearly all of this material was organic matter, in which bivalve mollusks of the genus *Mya* predominated in both numbers and volume (Table 6).

Table 3.—Frequency of occurrence, number of individuals, and volume of prey in stomach contents of 13 walruses taken near the western end of St. Lawrence Island, April-May 1975.

Prey type (genus)	Frequency of occurrence (/13)	Individuals		Volume	
		No.	%	ml	%
Priapulus	10	77	0.7	625	0.8
Nephthys	3	28	0.2	719	1.0
Lumbrinereis	2	44	0.4	22	tr
Echiurus	7	10	0.1	18	tr
Golfingia	4	62	0.6	215	0.3
Balanus	1	1	tr	1	tr
Anonyx	1	6	tr	2	tr
Ampelisca	1	2	tr	1	tr
Hippomedon	1	1	tr	1	tr
Argis	1	15	0.1	43	0.1
Sclerocrangon	2	39	0.4	118	0.2
Pagurus	2	2	tr	2	tr
Hyas	10	245	2.2	2,260	3.0
Neptunea	10	236	2.1	644	0.9
Buccinum	8	38	0.3	118	0.2
Natica	6	13	0.1	15	tr
Polinices	8	26	0.2	38	tr
Nudibranchia	1	1	tr	1	tr
Serripes	7	431	3.9	6,957	9.3
Clinocardium	6	78	0.7	1,048	1.4
Hiatella	3	7,586	68.8	7,375	9.9
Mya[1]	13	1,992	18.0	33,288	44.6
Octopus	1	1	tr	7	tr
Cucumaria	10	92	0.8	1,979	2.7
Animal fragments[2]	13	—	—	17,626	23.6
Inorganic sediments	13	—	—	1,525	2.0
Totals		11,026		74,648	

[1]Includes specimens misidentified as *"Spisula"* by Fay et al. (text footnote 3).
[2]Includes 1,095 ml of molluscan fragments not identifiable to genus.

Table 4.—Frequency of occurrence, number of individuals, and volume of prey in stomach contents of 14 walruses taken near the northern coast of St. Lawrence Island, May-June 1974-75.

Prey type (genus)	Frequency of occurrence (/14)	Individuals		Volume	
		No.	%	ml	%
Priapulus	8	75	1.4	451	0.4
Nephthys	5	12	0.2	107	0.1
Lumbrinereis	1	1	tr	1	tr
Echiurus	8	41	0.8	254	0.2
Golfingia	3	23	0.4	78	0.1
Argis	2	15	0.3	36	tr
Pagurus	4	6	0.1	9	tr
Hyas	9	74	1.4	338	0.3
Chionoecetes	1	2	tr	4	tr
Neptunea	10	141	2.6	201	0.2
Buccinum	6	10	0.2	16	tr
Natica	2	3	tr	2	tr
Polinices	8	71	1.3	68	0.1
Margarites	1	6	0.1	1	tr
Serripes	11	1,862	33.9	33,190	28.7
Clinocardium	3	110	2.0	1,434	1.2
Tellina/Macoma	2	31	0.6	68	0.1
Hiatella	1	1	tr	1	tr
Mya[1]	12	2,944	53.6	58,454	50.6
Cucumaria	9	52	1.0	810	0.7
Pelonaia	1	4	0.1	15	tr
Tunicate (cf. *Tethyum*)	1	1	tr	9	tr
Animal fragments[2]	14	—	—	19,242	16.6
Inorganic sediments	13	—	—	841	0.7
Totals		5,485		115,630	

[1]Includes specimens misidentified as *"Spisula"* by Fay et al. (text footnote 3).
[2]Includes 1,095 ml of molluscan fragments not identifiable to genus.

Table 5.—Frequency of occurrence, number of individuals, and volume of prey in stomach contents of seven walruses taken near Nome, May-June 1975.

Prey type (genus)	Frequency of occurrence (/7)	Individuals		Volume	
		No.	%	ml	%
Priapulus	5	16	0.1	99	0.4
Nephthys	1	2	tr	7	tr
Argis	1	1	tr	10	tr
Sclerocrangon	1	1	tr	6	tr
Neptunea	5	71	0.6	46	0.2
Natica	3	49	0.4	50	0.2
Polinices	5	45	0.4	77	0.3
Serripes	6	11,399	97.7	18,134	72.6
Tellina	6	65	0.6	175	0.7
Mya[1]	2	10	0.1	39	0.2
Animal fragments[2]	7	—	—	6,294	25.2
Inorganic sediments	1	—	—	45	0.2
Totals		11,659		24,982	

[1]Includes specimens misidentified as *"Spisula"* by Fay et al. (text footnote 3).
[2]Includes 10 ml of molluscan fragments not identifiable to genus.

Table 6.—Frequency of occurrence, number of individuals, and volume of prey in stomach contents of two walruses taken in the vicinity of King Island, June 1976.

Prey type (genus)	Frequency of occurrence (/2)	Individuals		Volume	
		No.	%	ml	%
Nephthys	1	1	0.2	5	tr
Echiurus	2	2	0.3	2	tr
Hyas	1	2	0.3	3	tr
Natica	1	2	0.3	2	tr
Serripes	1	10	1.6	31	0.2
Tellina/Macoma	1	1	0.2	1	tr
Hiatella	1	5	0.8	1	tr
Mya[1]	2	590	94.6	16,223	87.6
Cucumaria	2	11	1.8	143	0.7
Animal fragments	2	—	—	2,117	11.4
Inorganic sediments	2	—	—	7	tr
Totals		624		18,535	

[1]Includes specimens misidentified as *"Spisula"* by Fay et al. (text footnote 3).

Bering Strait.— Stomach contents were obtained from 56 males and 15 females in volumes ranging from 0.1 to more than 26.5 kg (mean, 8.1 kg) per stomach. Most of these materials were parts of mollusks, predominantly *Serripes*, *Hiatella*, and *Mya* (Table 7). Unique in this sample was the occurrence in one stomach of remains of a bearded seal, *Erignathus barbatus*, including pieces of skin, blubber, muscle, liver, heart, and pancreas. One other stomach, not quantitatively analyzed, contained a high proportion of large actiniarian coelenterates, possibly of the genus *Metridium*.

General Observations.—Whole shells, even of the smallest bivalves, were uniformly scarce to absent in the samples of stomach contents. Shell fragments, most of which were bits broken from the rim of the valves, were present in 42% of the stomachs but comprised only trace amounts (< 0.1% by volume of the total ingesta). Nearly all of the feet and siphons were entire, showing no signs of mastication.

For the most part, each of the nonmolluscan invertebrates appeared to have been swallowed whole, without mastication. However, they frequently showed signs of having been subjected to local compression, perhaps by the lips of the walrus, before they were swallowed. The exoskeletons of all of the brachyuran crabs were very soft and flexible, suggesting that these crabs had molted just before the time of ingestion. That their softness was not the result of digestion was indicated by the hard, calcareous quality of a fragment of lithodid crab shell found in one stomach. Presumably, this small piece (from the carapace of *Paralithodes* sp.) had been ingested accidentally, along with the inorganic solids.

Table 7.—Frequency of occurrence, number of individuals, and volume of prey in stomach contents of 71 walruses taken in Bering Strait, May-June 1975.

Prey type (genus)	Frequency of occurrence (/71)	Individuals		Volume	
		No.	%	ml	%
Priapulus	26	70	0.1	889	0.2
Nephthys	26	267	0.4	3,499	0.6
Lumbrinereis	4	49	0.1	71	tr
Pectinaria	2	2	tr	2	tr
Echiurus	6	27	tr	268	tr
Golfingia	28	991	1.5	3,215	0.6
Anonyx	7	33	tr	24	tr
Lembos	2	3	tr	2	tr
Argis	2	4	tr	2	tr
Pagurus	7	18	tr	45	tr
Hyas	13	23	tr	109	tr
Neptunea	47	721	1.1	4,980	0.9
Buccinum	41	303	0.5	759	0.1
Natica	31	156	0.2	200	tr
Polinices	30	542	0.8	695	0.1
Margarites	1	2	tr	1	tr
Serripes	62	2,145	3.3	47,906	8.4
Yoldia	10	919	1.4	339	0.1
Nucula	1	2	tr	1	tr
Tellina/Macoma	11	1,269	2.0	1,413	0.2
Hiatella	51	41,371	63.8	57,645	10.1
Astarte	2	2	tr	2	tr
Mya[1]	66	15,840	24.4	373,721	65.2
Octopus	2	2	tr	45	tr
Cucumaria	9	63	0.1	1,502	0.3
Psolus	7	22	tr	554	0.1
Erignathus	1	1	tr	10,498	1.8
Animal fragments[2]	67	—	—	53,051	9.3
Inorganic sediments	69	—	—	11,308	2.0
Totals		64,847		572,746	

[1]Includes specimens misidentified as *"Spisula"* by Fay et al. (text footnote 3).
[2]Includes 385 ml of molluscan fragments not identifiable to genus.

Inorganic sediments occurred with the organic ingesta in all but 9 of the 107 stomachs from St. Lawrence Island to Bering Strait. These ranged in amounts from 1 to 1,040 ml/stomach and consisted mainly of sand and gravel, with a few stones up to 3 cm in diameter. Probably, some of the molluscan shell fragments also were ingested with the gravel, for broken shells make up a significant part of the sediments in this region. Two items of human origin (from ocean dumping) also were recovered from the stomachs: A 3 × 4 cm piece of bottle glass, and a 1 × 5 cm fragment of fiber gasket material.

In Bering Strait and west of St. Lawrence Island, where both males and females were sampled, the females tended to feed on the smaller kinds of bivalves, especially *Hiatella*; the males had fed more on the largest ones, especially *Mya* (Table 8). The single female taken at King Island contained approximately the same kinds of prey as did the subadult male. Where the females had fed on the same kinds of prey as the males, they tended to take individuals of smaller size than did the males (Table 9). Thus, the stomachs of the females tended to contain larger numbers of prey but generally smaller volumes of ingesta than did those of the males (Fig. 2). The prey in the stomachs of males tended to be about 6 times larger than those in the stomachs of females. The largest number of individual prey in one stomach was 6,401 in an adult female taken in Bering Strait. Nearly all of those were *Hiatella arctica*. The smallest number was three, in the adult male that had fed on one bearded seal and two bivalves.

Table 8.—Comparative percentage by weight of bivalve prey in the stomachs of males and females, northern Bering Sea, spring 1974-76.

	Locality, sex, and sample size							
	W. of St. Lawrence		N. of St. Lawrence		King Island		Bering Strait	
Prey type (genus)	♂ $n=10$	♀ $n=3$	♂ $n=13$	♀ $n=1$	♂ $n=1$	♀ $n=1$	♂ $n=56$	♀ $n=15$
Hiatella	<0.1	80.8	<0.1	0	0	<0.1	6.9	51.8
Mya	69.6	11.3	61.2	0	99.2	97.3	80.0	32.6
Cockles[1]	17.3	0	36.2	50.0	0	0.1	9.8	7.9
Tellinids[2]	0	0	0.1	0	<0.1	0	<0.1	2.5
Other small clams[3]	0	0	0	0	0	0	<0.1	0.5

[1]*Serripes* and *Clinocardium*.
[2]*Tellina* and *Macoma*.
[3]*Yoldia*, *Nucula*, and *Astarte*.

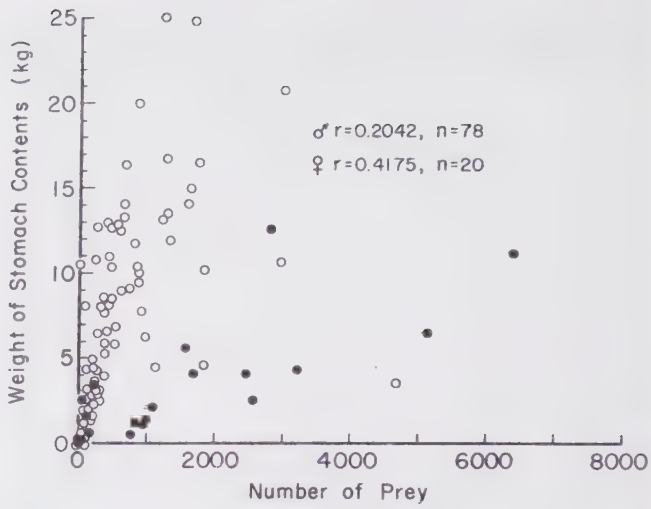


Figure 2.—Tendency for correlation between numbers and volumes of prey in stomachs of male (open circles) and female (solid circles) walruses taken in the St. Lawrence Island to Bering Strait region, spring 1974-76. The tendency for difference between sexes is not significant.

DISCUSSION

The Pacific walrus population inhabits the pack ice of the Bering Sea in winter, mainly to the south of St. Lawrence Island and in outer Bristol Bay (Braham et al. 1984). The period of winter residence in the Bering Sea appears to be the mating season for these walruses (Fay et al. 1984). The availability of an adequate supply of food in that period may be of critical importance only to the adult females, who are supporting dependent young and/or carrying a fetus. The adult males appear to fast during much of the winter; they apparently feed intensively only in spring, summer, and autumn, when they mostly reside in other areas (Fay 1982).

The information on availability of food in the wintering areas is meager; as is the complementary information on the walruses' feeding habits at that time. The only samples of walrus food in the north-central wintering area, south of St. Lawrence Island, are from the contents of one stomach, plus five fecal samples from the ice and a few items dropped on the ice beside breathing holes. Together, these suggest that the diet there is made up of a wide assortment of bivalves, gastropods, crustaceans, echiurids, and tunicates in about equal amounts. Because the bivalves mostly have no indigestible parts (other than the shells, which are not eaten by the walruses), they probably are underrepresented in fecal analyses. According to the work of Stoker (1978), the most abundant bivalves in the north-central wintering area are *Macoma calcarea*, *Nucula tenuis*, *N. radiata*, *Yoldia hyperborea*, and *Serripes groenlandicus*. The first four of these made up more than 56% by weight of the biomass of macrobenthos in Stoker's samples, yet to the best of our present knowledge, they seldom are eaten by walruses when other, larger prey are available. Of the apparently preferred, larger bivalves, such as *Serripes* and *Mya*, Stoker's samples indicated occurrence only in small amounts (< 5% of the biomass). Because of known deficiencies of the sampling gear (0.1 m² Van Veen grab), however, this may not be a reliable indication of abundance. Since it is clear that this north-central area is occupied by about two-thirds to three-fourths of the walrus population during winter and spring (Kenyon

Table 9.—Comparative unit weights (g/individual) of prey in the stomach contents of male and female walruses, northern Bering Sea, spring 1974-76.[1]

	W. of St. Lawrence				N. of St. Lawrence				King Island				Bering Strait			
	♂		♀		♂		♀		♂		♀		♂		♀	
	No.	Unit	No.	Unit	No.	Unit	No.	Unit	No.	Unit	No.	Unit	No.	Unit	No.	Unit
Polychaetes	72	10.3	0	—	13	8.3	0	—	1	(5)	0	—	214	14.0	104	5.6
Sipunculids	6	1.8	56	3.6	23	3.4	0	—	0	—	0	—	912	3.3	79	2.6
Echiurids	6	1.2	4	2.8	41	6.2	0	—	1	(1)	1	(1)	19	9.4	8	11.1
Priapulids	47	5.5	30	12.3	75	6.0	0	—	0	—	0	—	58	13.6	12	8.5
Gastropods	283	2.4	30	4.5	192	1.3	39	0.8	0	—	2	1.0	1,177	4.7	547	2.1
Cockles	509	15.7	0	—	1,966	17.6	6	5.3	0	—	10	3.1	1,486	29.5	659	6.2
Mya	1,904	16.9	88	11.7	2,944	19.8	0	—	400	32.2	190	17.6	14,924	23.9	915	18.5
Hiatella	47	0.4	7,539	1.0	1	(1)	0	—	0	—	5	0.2	22,538	1.4	18,833	1.4
Tellinids	0	—	0	—	31	2.2	0	—	1	(1)	0	—	39	2.5	1,230	1.1
Other small clams	0	—	0	—	0	—	0	—	0	—	0	—	188	0.5	735	0.3
Shrimps	54	3.0	0	—	15	2.4	0	—	0	—	0	—	0	—	4	0.5
Crabs	246	9.2	1	(1)	82	4.3	0	—	0	—	2	1.5	35	3.5	6	5.3
Holothureans	91	21.7	1	(6.0)	52	15.6	0	—	5	17.6	6	9.2	73	24.3	12	23.7
Overall	3,265	14.2	7,749	1.2	5,435	17.6	45	1.4	408	31.8	216	15.9	41,663	10.7	23,144	2.8

[1]Sample from Nome area excluded, since only male walruses were taken there.

1960,[5] 1972;[6] Braham et al. 1984), we presume that the benthic stocks are larger than were indicated by Stoker's samples.

Substantially more information is available from the walruses in the southeastern Bering Sea in winter, but the sample is nonetheless very small and is mainly from one small part of that region. In January, March, and April, the cockle *S. groenlandicus* and whelks of the genera *Neptunea* and *Buccinum* appear to be most heavily utilized. A high proportion of molting tanner crabs (*Chionoecetes* spp.) also has been found in the stomach contents and feces. Tikhomirov (1964:283) collected a series of 50 walruses in this same region in March-April 1962 and reported that they had fed mainly on "shrimps and crabs, among which were found a few *kamchatki* [king crab, *Paralithodes camtschatica*], and to a lesser degree, mollusks." He remarked on the contrast between these and the stomach contents of walruses taken in the Chukchi Sea in summer, "where the principal food . . . is mollusks." According to Stoker's (1978) data, the dominant (by weight) bivalves in this southeastern region are *Macoma calcarea* and *Astarte borealis*, which made up more than 32% of the biomass of macrobenthos in his samples. *Serripes groenlandicus* comprised about 3.5%.

The feeding habits of walruses farther east in Bristol Bay are unknown. This is clearly an important breeding and feeding area in some winters and supports several thousand males throughout the summer. The possibility of competition there between the walruses and a potential clam fishery is under investigation. Adequate stocks for support of a clam fishery appear to be present only in the southern part of Bristol Bay (Hughes et al. 1977[7]), which may be outside the normal range of most of the walruses. There, in the nearshore waters, the stocks of the two species of interest to the fishery, *Spisula polynyma* and *Tellina lutea*, are more than 10 times greater than in the northern parts of the Bay.

The largest volume of data on the feeding relationships of walruses in the Bering Sea is from the northernmost sector, between St. Lawrence Island and Bering Strait. In the past, this region was utilized by walruses mainly during their northward migration in spring and southward migration in autumn. Since 1971, however, it also has become an important summering area for a significant part of the population. Previous information from this region, provided by Nikulin (1941) and Brooks (1954), indicated that bivalves (especially *Mya*) were the principal foods there in spring and early summer. Our data from 1975 tend to confirm that: The stomach contents of walruses taken in the western and northern parts of this region contained mainly *Mya* and *Hiatella*; in the eastern part *Serripes* was dominant. Stoker's (1978) bottom samples from this region confirmed the abundance of *Serripes* in the standing stocks of the eastern sector, but they did not reflect an abundance of either *Mya* or *Hiatella* in the west or north. Presumably, this again was a deficiency of the sampling gear, which did not function well in the predominantly rocky to gravelly substrates.

With the prospect of increasing human impact on the environment of the walrus population through expanded fisheries (including clam and snail fisheries) and development of mineral and petroleum resources on the continental shelf of the Bering Sea, the need for greater knowledge of the animals themselves and of their environment also will increase. For management of our mutually important walrus resource, we shall need to know a great deal more about the feeding relationships of this animal and the benthic stocks on which it relies. One might ask, for example, how dependent is the walrus population on the bivalves that make up the bulk of its diet right now? If those are depleted by commercial development or pollution, can the walrus population persist in a productive mode by switching to other benthic resources not presently utilized? If so, what effects would this have on other marine vertebrates (e.g., fishes, seals) that may already utilize those same resources? Future research in support of an effective multispecies management policy for the Bering Sea will need to examine such relationships in detail.

[5]Kenyon, K. W. 1960. Aerial surveys of marine mammals in the Bering Sea, 23 February to 2 March 1960 and 25-28 April 1960. Unpubl. rep., 39 p. U.S. Bur. Sport Fish. Wildl., Seattle, WA 98115.

[6]Kenyon, K. W. 1972. Aerial surveys of marine mammals in the Bering Sea, 6-16 April 1972. Unpubl. rep., 79 p. U.S. Bur. Sport Fish. Wildl., Seattle, WA 98115.

[7]Hughes, S. E., R. W. Nelson, and R. Nelson. 1977. Initial assessments of the distribution, abundance, and quality of subtidal clams in the S.E. Bering Sea. Processed rep., 43 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

ACKNOWLEDGMENTS

For assistance in acquisition of several of the samples reported, we are grateful to the following personnel of the Alaska Department of Fish and Game: John J. Burns, Kathryn J. Frost, Karl Grauvogel, Lloyd F. Lowry, and Edward Muktoyuk. We thank also the U.S. Coast Guard for logistic support during the Arctic Winter West cruises of the CGC *Northwind* in 1970, the CGC *Glacier* in 1971, and the CGC *Burton Island* in 1972, and the Sakhalin Fishing Fleet (SAKHRYBFLOT) for support during the Soviet-American research cruise of the ZRS *Zagoriany* in 1976. The American studies were supported in part by funds from the University of Alaska Sea Grant Program, NOAA Office of Sea Grant, Department of Commerce, under grants GH-83, I-36109, and 04-3-158-41, and in part by contracts MM4AC-006 and MM5AC-024 between the U.S. Marine Mammal Commission and the Institute of Marine Science, University of Alaska. The Soviet studies were supported by the Magadan Section of the Pacific Research Institute of Fisheries and Oceanography (MoTINRO).

LITERATURE CITED

BRAHAM, H. W., J. J. BURNS, G. A. FEDOSEEV, and B. D. KROGMAN.
1984. Habitat partitioning by ice-associated pinnipeds: Distribution and density of seals and walruses in the Bering Sea, April 1976. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:25-47.

BROOKS, J. W.
1954. A contribution to the life history and ecology of the Pacific walrus. M.S. Thesis, University of Alaska, Fairbanks, 103 p.

CHAPSKII, K. K.
1936. The walrus of the Kara Sea. Tr. Svesoyuz. Arkt. Inst. 67:1-124.

FAY, F. H.
1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North Am. Fauna 74, 279 p. U.S. Fish Wildl. Serv., Washington, D.C.

FAY, F. H., G. C. RAY, and A. A. KIBAL'CHICH.
1984. Time and location of mating and associated behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:89-99.

KRYLOV, V. I.
1965. Determination of age, rate of growth, and analysis of the age structure of the harvest of Pacific walruses. *In* E. N. Pavlovskii, B. A. Zenkovich, S. E. Kleinenberg, and K. K. Chapskii (editors), Marine mammals, p. 201-211. Nauka, Moscow.
1971. On the food of the Pacific walrus (*Odobenus rosmarus divergens* Ill.). *In* E. S. Mil'chenko, T. M. Andreeva, and G. P. Burov (editors), Studies of marine mammals. Tr. AtlantNIRO 39:110-116.

MANSFIELD, A. W.
1958. The biology of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus), in the eastern Canadian Arctic. Ph.D. Thesis, McGill University, Montreal, PQ, Canada, 146 p.

NIKULIN, P. G.
1941. The Chukchi walrus. Izv. TNIRO 20:21-59.

STOKER, S. W.
1978. Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi seas. Ph.D. Thesis, Univ. Alaska, Fairbanks, 259 p.
TIKHOMIROV, E. A.
1964. On the distribution and biology of pinnipeds of the Bering Sea. *In* P. A. Moiseev, A. G. Kaganovskii, and I. V. Kisevetter (editors), Soviet fisheries investigations in the northeastern part of the Pacific Ocean, Pt. 3, p. 277-285. Pischevaya Promyshlennost', Moscow.
VIBE, C.
1950. The marine mammals and the marine fauna in the Thule District (Northwest Greenland) with observations on ice conditions in 1939-41. Medd. Grønl. 150(6):1-115.

Time and Location of Mating and Associated Behavior of the Pacific Walrus, *Odobenus rosmarus divergens* Illiger

FRANCIS H. FAY,[1] G. CARLETON RAY,[2] and ARKADII A. KIBAL'CHICH[3]

ABSTRACT

Management of the Pacific walrus population by the Soviet Union and the United States has been based up to now on several untenable assumptions concerning the time and place of mating, the social system during the mating season, and the sex and age composition of the population. The condition of reproductive organs of males and females taken throughout the late autumn, winter, and spring indicates that the principal period of mating is January-February, rather than April-June as has been assumed. During late winter, virtually all of the adult females and most of the adult males are situated in the north-central and southeastern pack ice of the Bering Sea. The sex ratio of adults in those areas is about 1 male:10 females. Most of the subadult males are in peripheral and intervening areas. Adult females and young within the two concentration areas in March associate in tightly knit herds, which move about apparently in search of food and in response to movements of the pack ice. One or more adult males associates with each such herd. These bulls engage in ritualized visual and acoustical displays in the water, especially when the females are at rest on ice. While displaying, they maintain a distance of about 5 to 10 m from each other; closer intrusion is met by threat, followed by fighting. Individual females enter the water and engage in facial and bodily contact with the displaying males, after which, presumably, copulation takes place underwater. The social organization appears to be unique among otarioid pinnipeds, more closely resembling a lek than a "harem" system.

РЕЗЮМЕ

Регулирование популяции тихоокеанского моржа производимое Советским Союзом и США основывалось на некоторых несостоятельных предположениях касающихся времени и места спаривания, поведения и полового состава популяции в этих районах. Сведения полученные во время осмотра половых органов самок и самцов, взятых поздней осенью, зимой и весной, указывают что основной период спаривания протекает в январе - феврале, а не в апреле - июне, как это считалось ранее. Поздней зимой почти все взрослые самки и самцы обитают на северо-центральном и юго-восточном паковом льду Берингова моря. Половая пропорция в этих местах почти 1 самец: 10 самок. Большинство созревающих самцов находится в периферийных районах. Взрослые самки с молодняком собираются в этих районах в марте в плотные стаи и добывая пищу постепенно продвигаются со льдами. Один или несколько взрослых самцов опекают одну из таких групп, издавая при этом ритуальные звуки и взгляды из воды, когда самки отдыхают на льду. В это время самцы сохраняют держатся друг от друга на расстоянии от 5 до 10 м., а при вторжении начинается преследование и драки. Самки по одиночке сходят в воду прикасаются лицом и телом к самцам коопулируют с ними под водой. Более молодые самцы, которые позже приходят в течку, чем взрослые самцы, вероятно оплодотворяют тех самок, которые овулируют после окончания пика спаривания.

INTRODUCTION

The formulation of a management plan for any species requires a thorough knowledge of its natural history, reproductive biology, and population structure. Management of the Pacific walrus, *Odobenus rosmarus divergens*, by both the United States and the Soviet Union has been founded on several basic but inadequately tested assumptions.

1) Walruses are polygynous. Walrus are gregarious and sexually dimorphic, characters typical of polygynous mammals (Nutting 1891; Bertram 1940; Bartholomew 1970; Trivers 1972; Stirling 1975; Ralls 1977). Their closest relatives, the fur seals and sea lions (Otariidae) have these characters and are polygynous. However, the otariids congregate on land to mate and bear young, whereas the walrus accomplishes these functions on or near sea ice. The possibility that walruses are monogamous has been proposed by some investigators (Allen 1880; Krylov 1968), apparently on the basis of frequent sightings of small "family groups" during and after the calving period. This proposal has been widely accepted in the Soviet Union but not in the United States. However, the only support for either view has been by inference.

2) The sex ratio of adults is about 1:1. Substantial data on the sex ratio of newborn walruses indicate that there are about as many males as females at birth (Nikulin 1941; Brooks 1954; Burns 1965[4]). Representative samples of adults have not been available, however,

[1]Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, USA.
[2]Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903, USA.
[3]All-Union Institute of Fisheries and Oceanography (VNIRO), Laboratory for Marine Mammal Investigations, Moscow 107140, USSR.

[4]Burns, J. J. 1965. The walrus in Alaska, its ecology and management. Alaska Dep. Fish Game, Juneau, 48 p.

since the sexes tend to segregate during most of the year. Because of differential availability and vulnerability of the sexes to hunting, and because of various preferences among hunters, harvest samples tend to be strongly biased and cannot be assumed to be representative of the population as a whole (Burns footnote 4; Krylov 1965; Gol'tsev 1968). Thus, the sex ratio of the breeding adults is unknown.

3) Mating takes place in April to June. All other pinnipeds, as far as is known, mate within a few days or weeks after giving birth. It has been assumed that walruses are not different. Calves are born mainly in the month of May (Krylov 1966[5]), and by extrapolation from the size of fetuses obtained in summer and autumn, implantation of the blastocyst has been estimated to occur mainly in June (Chapskii 1936; Mansfield 1958). The findings of Brooks (1954), Burns (footnote 4), and Krylov (1969) have confirmed this and have shown that some females have large Graffian follicles at that time. Thus, it has been presumed that mating takes place about the same time as birth, that pregnancy lasts about 11 or 12 mo, and that, unlike the other pinnipeds, there is no delay in implantation (Harrison 1969).

4) There is a "surplus" of males. Given that the sex ratio at birth is about 1:1, and that there is a high probability of polygyny, there may be a large "surplus" of males that could be harvested without adversely affecting recruitment of males into the breeding population. This is the basis of management of other polygynous species, especially the northern fur seal, *Callorhinus ursinus* (Roppel and Davey 1965), and it has been at the foundation of management also of the Pacific walrus population in both the United States and the Soviet Union.

The principal weakness in these assumptions lies in their inconsistency with each other and with other relevant findings. For example, while the sex ratio at birth in most species of mammals is about 1:1, the ratio in the adults usually is unequal (Glucksmann 1974). In marine mammals that are strongly polygynous, adult females greatly outnumber adult males (Carrick et al. 1962; Chapman 1964; Ralls et al. 1980). If walruses are monogamous, their adult sex ratio should be near parity; if they are polygynous, then adult females should be considerably more numerous than adult males.

It is now clear that female walruses usually breed at 2- to 3-yr intervals, and that less than half of them bear young in any given year (Freiman 1941; Brooks 1954; Mansfield 1958; Loughrey 1959;[6] Krylov 1962, footnote 5; Burns footnote 4). This suggests that the period of gestation is longer than 1 yr and points to the possibility of an earlier (than April-June) mating season. The latter was implied also by Mansfield's (1958) finding of fertile adult males in late November and March, and by Fay's (1955) observations that the testes of adult males in April-June were mainly in retrogressive stages.

Because less than half of the females breed in a given year, there could be a large "surplus" of males, if the adult sex ratio is 1:1. Conversely, if walruses are polygynous, differentially high mortality of males from natural causes is probable (Ralls et al. 1980), which could result in a more balanced sex ratio of breeders or in a "surplus" of females. Only 3 to 14% of male elephant seals, *Mirounga angustirostris*, survive to sexual maturity (Le Boeuf 1974); in northern fur seals, *Calorhinus ursinus*, the natural mortality rate of males is more than three times that of females (Chapman 1964; Johnson 1968). The concept of "surplus" deserves careful examination.

In our work, both jointly and separately, over the past several years, we have gathered new data pertaining to the time and place of mating, composition of the breeding adult segment of the population, and social behavior of the mating groups. We present that information here as a contribution to clarification of these matters, which are of vital importance for managing the Pacific walrus population on an international basis.

METHODS

We obtained information on the time and place of mating and associated behavior, first, by examination of reproductive organs of walruses taken throughout the winter, spring, and summer; second, by visual and photographic methods during aerial surveys; third, by observation of animals via icebreaking ships; and fourth, by acoustical methods.

Fay obtained testes and epididymides from 111 juvenile, subadult, and adult males at St. Lawrence Island in November to June and at Barrow in July and August 1952 to 1963. Testes were weighed, and tissue samples were fixed in 10% Formalin [7] or AFA, embedded in paraffin, sectioned on a rotary microtome at 7 to 10 μ, stained with hematoxylin-eosin, and mounted on glass slides. These were examined microscopically to determine seasonal stages of development of the seminiferous epithelium and the period when spermatozoa were present in the epididymal tubules. Kibal'chich obtained testes from 115 juvenile, subadult, and adult males in the southeastern Bering Sea during March-April 1976 via the joint Soviet-American research cruise of the ZRS *Zagoriany*. These were weighed to the nearest gram, and the presence or absence of spermatozoa was determined microscopically by the impression smear method at the time of collection.

Fay obtained reproductive tracts from 218 adult females taken in the north-central Bering Sea from November to June 1952 to 1972. The ovaries from these were fixed and stored whole in 10% Formalin for 1 to 3 mo, then sliced into 1 to 2 mm thick serial sections. They were examined without magnification, to determine the number and size of vesicular follicles and the size and state of development of corpora lutea. Gol'tsev (1978)[8] obtained reproductive tracts from 34 adult females, during the ZRS *Zagoriany* cruise, and treated them in essentially the same way. In all instances, age of the animals was determined from counts of cementum layers in thin sections of the cheek teeth, as described by Mansfield (1958) and Krylov (1965).

Information on the geographical location of the animals during and just after the mating season was obtained mainly from unpublished aerovisual survey data made available by K. W. Kenyon, G. A. Fedoseev, J. J. Burns, and H. W. Braham. These surveys were made during February to April of 1960 to 1972. Additional aerial survey data were obtained by Ray, during flights over the Bering Sea ice in April 1975 and 1976 via National Aeronautics and Space Administration remote-sensing aircraft. These were supplemented

[5]Krylov, V. I. 1966. Time of calving and mating of the Pacific walrus. [Abstr.] Third all-union conf. stud. marine mammals, p. 28-29. VNIRO, Vladivostok.

[6]Loughrey, A. G. 1959. Preliminary investigation of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus). Can. Wildl. Serv., Wildl. Manage. Bull. (Ser. 1) No. 14, 123 p. Queen's Printer, Ottawa.

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[8]Gol'tsev, V. N. 1978. Materials on reproduction of the Pacific walrus. Abstracts 7th all-union conf. marine mammals, p. 89. Ministerstro Rybnogo Khozyaistva SSSR, Moscow.

by surface observations via iceworthy ships in March-April 1971 (CGC *Glacier*), February-March 1972 (CGC *Burton Island*), and March-April 1976 (ZRS *Zagoriany*).

Direct observations of social behavior were made by Fay and Ray during March 1972 and April 1971 via the CGC *Burton Island* and CGC *Glacier*, respectively, in the north-central Bering Sea, and in April to June 1952 to 1966 via small boats in the vicinity of the western end of St. Lawrence Island. Kibal'chich and Fay observed social behavior of walruses in the southeastern Bering Sea via the ZRS *Zagoriany* in March-April 1976.

RESULTS

Time of Mating

Data from the reproductive organs of males taken in the northern Bering and Chukchi Seas in November to August 1952 to 1963 (Table 1) indicate that 1) the mature adults, 17 to 37 yr old, were most often fertile, principally in the period November to February, 2) the younger adults, 12 to 16 yr old, were fertile less often and over a longer period, and 3) the subadults, 5 to 11 yr old, were least often fertile, and their highest fertility occurred about 2 mo later than for the mature males. The cycle of testis weights suggests a peak in development in December or January for the older males and in February or March for the younger individuals (Fig. 1). None of the

Table 1.—Number of male walruses examined (*n*) and percentage in which seminiferous tubules contained spermatozoa in bi-monthly samples from the northern Bering and Chukchi Seas, 1952-63.

Age class (yr)	November-December		January-February		March-April		May-June		July-August	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%
5-11	14	14	3	67	5	40	9	44	3	0
12-16	18	72	3	67	4	50	14	50	5	0
17-37	6	100	3	100	8	25	10	10	6	0

animals younger than 10 yr old had spermatozoa in the epididymides; spermatozoa were present in a few of the 10 to 13 yr olds from December to May and in most of the fertile mature males from November to May. By analogy with other pinnipeds and with other carnivores in general, in which the principal mating period is just after the peak of the testis cycle of the mature males (Asdell 1964; Harrison 1969), these findings suggest that the mating of walruses takes place in mid-winter, rather than in spring.

Data obtained from males collected in the southeastern Bering Sea between 20 March and 11 April, during the Soviet-American cruise of the ZRS *Zagoriany*, confirmed this in part (Gol'tsev footnote 8). Spermatozoa were most often present in the testes of animals 11 to 19 yr old (71% fertile), whereas the testes of most of the other mature males, 17 to 32 yr old, were flaccid and in a retrogressive state. Those of the subadults, 8 to 10 yr old, were mainly in the beginning stages of spermatogenesis.

The data from 88 sexually mature females that were not carrying a large fetus and had not given birth recently (i.e., within 2 mo) are shown in Table 2. Again, the samples per month are small, but the trends seem clear. Their implication is that 1) ovulation may begin as early as December or take place as late as May in some individuals, as indicated by the presence in the ovaries of vesicular follicles larger than 10 mm in diameter, and 2) that fertilization is essentially completed by March, as indicated by the presence of a new corpus

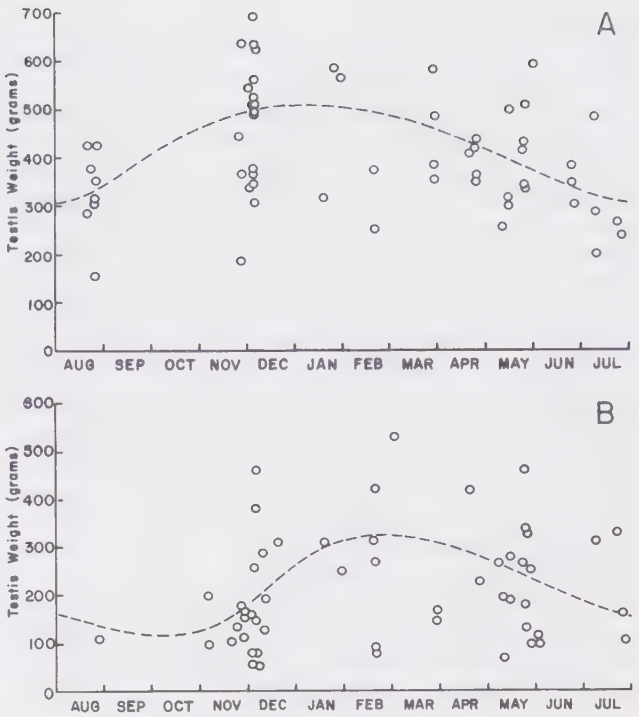


Figure 1.—Weight in grams of one testis from each of 109 male walruses taken in the northern Bering and Chukchi Seas, in relation to date of collection. A) Males 14 to 37 yr old; B) males 5 to 13 yr old. Each symbol represents one specimen. Curves are visually estimated means.

Table 2.—Results of examination of ovaries from female walruses that were not carrying a large fetus and had not recently given birth (northern Bering Sea 1952-63; southeastern Bering Sea 1976).

Month	Number examined	Findings in ovaries: Follicles < 10 mm diam.		Follicles > 10 mm diam.		New corpus luteum	
		n	%	*n*	%	*n*	%
November	1	1	100	0	—	0	—
December	13	12	92	1	8	0	—
January	2	2	100	0	—	0	—
February	2	1	50	0	—	1	50
March	12	3	25	0	—	9	75
April	15	4	27	0	—	11	73
May	33	5	15	4	12	24	73
June	10	1	10	0	—	9	90

luteum of pregnancy. All but two of the corpora lutea of these animals taken in February to June already were fully luteinized; one from a specimen taken in early April and one in mid-February were incompletely formed, indicating that fertilization had taken place about 2 wk earlier.

The remaining 164 females that we examined in November to June were either carrying a large fetus (November-April) or had recently given birth (April-June). Only one of these, taken in June, had a follicle larger than 10 mm in its ovaries, and none had any new corpora lutea of pregnancy like those in the foregoing group.

Thus, our data from both the males and the females indicate that the period of mating in the Pacific walrus population is principally in mid-winter, probably beginning no earlier than December and ending no later than March.

Location of Mating

Five aerial surveys of the Pacific walrus population in its wintering area in the Bering Sea were conducted jointly by the U.S. Fish and Wildlife Service and the Alaska Department of Fish and Game between 1960 and 1972.[9] The principal objective of those surveys was to estimate the number of animals in the population, but they provided, at the same time, an overview of the animals' distribution in the pack ice. The greater part of the population was situated in the north-central Bering Sea, mainly to the south and southwest of St. Lawrence Island; most of the remainder was in the southeast, from the vicinity of Nunivak Island and Kuskokwim Bay to inner Bristol Bay (Fig. 2). In the intervening and peripheral areas, the animals occurred in low densities. Subsequent surveys in April 1975 and March-April 1976 by Wartzok and Ray (1980)[10] and by Braham et al. (1984), in general, confirmed those findings. The pattern as shown in Figure 2 is described only in the most general way, since the variations in ice conditions from year to year have a strong influence on it (Burns et al. 1980[11]).

From interpretation of aerial photographs taken during one of those surveys (1972) and from direct observations from ships, we have repeatedly determined that the two generalized areas of high density contain mostly females and young during March and April, whereas the intervening and peripheral areas contain mostly males (Table 3). The ratios of adult males to adult females in the north-central and southeastern areas of high density were about 1:10 and 1:8, respectively. In the low density areas, the ratio of males to females was about 27:1, and most of those males were subadults.

Thus, it is apparent that, during late winter to early spring, the Pacific walrus breeding population is essentially split into two groups, one of which is located in the north-central Bering Sea and the other is in the southeastern Bering Sea-Bristol Bay region. Further, there are strong indications that the sex ratio of the adult, breeding population contains many more females than males.

[9]K. W. Kenyon, Biologist, U.S. Fish Wildl. Serv., Bur. Sport Fish. Wildl., Seattle, WA 98115, pers. commun. 1960-72.

[10]Wartzok, D., and G. C. Ray. 1980. The hauling-out behavior of the Pacific walrus. PB 80-192 578, 46 p. Natl. Tech. Inf. Serv., Springfield, VA 22161.

[11]Burns, J. J., L. H. Shapiro, and F. H. Fay. 1980. The relationships of marine mammal distributions, densities, and activities to sea ice conditions. Final report, R.U. 248/249, 172 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

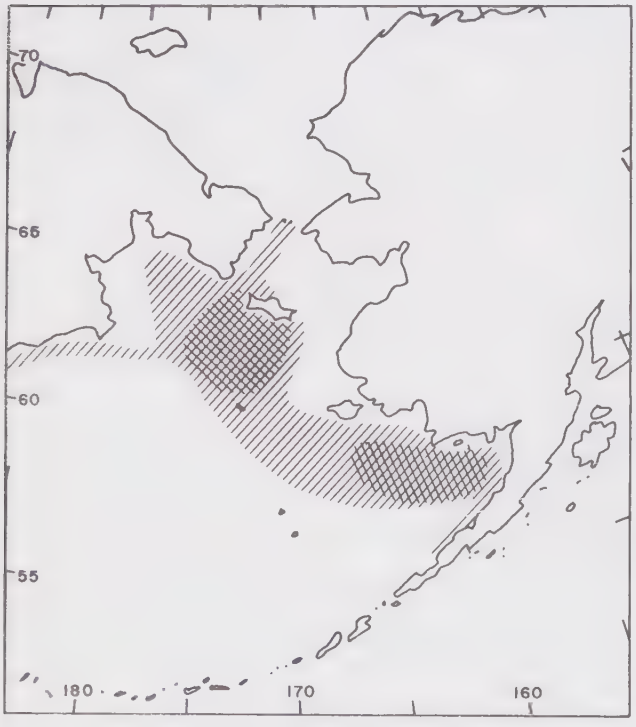


Figure 2.—Chart of the Bering Sea, showing the approximate average pattern of walrus distribution in mid- to late winter (hatched) and the two areas in which most of the females and adult males were found in mid-February to mid-April, 1960 to 1972 (cross-hatched).

Table 3.—Composition of visually and photographically surveyed walruses in Bering Sea during March-April 1971-76.

Area	Month	No. of animals	Immature (both sexes)	Subadults and adults	
				Males	Females
North-central	Mar.	907	251	90	566
North-central	early Apr.	332	[1]131	13	[1]188
North-central	mid-Apr.	1,171	[1]459	40	[1]672
East-central	mid-Apr.	255	4	[2]240	8
East-central	Mar.-Apr.	73	11	[2]54	8
Southeastern	mid-Apr.	621	[1]237	38	[1]346

[1]In original field data, adult females and immature males and females were not recorded separately. Numbers shown here were extrapolated from the totals, based on a sample of 857 animals in which 509 (59.4%) were identified as adult females and 348 (40.6%) as immature animals of both sexes.

[2]More than 75% of these were subadult males; at least 90% of all others listed were mature males.

Associated Behavior

Most of our data on herd structure and social and acoustical behavior are from the north-central high density area during March 1972 and April 1971. We obtained some additional behavioral information in the western perimeter of the southeastern area in March-April 1976. The following are resumés, presented in seasonal chronological order, of 13 instances in which we observed social behavior relevant to mating in mixed herds.

4 March 1972, 0700 to 0800 h, at Lat. 62°53′N, Long. 172°06′W.—We encountered about 330 animals in a large open water lead. About 295 of these were hauled out and most were sleeping in three groups of 20, 75, and 200 on three large floes in the center of the occupied area (Fig. 3a). Evidently, these groups had been lying in the same position for several hours, as many of the animals had deposits of frost on their exposed surfaces. About 80% of these animals were subadult and adult females; the rest were immature young, 1 to 4 or 5 yr old. Another group of about 15 females was in the water and apparently feeding, 0.3 km away in the same lead. We saw no adult bulls within any of the groups of females and young; however, there were 19 bulls in the vicinity, within a 0.5 km radius, and these were distributed as follows: 12 sleeping on the ice in groups of 6, 2, 1, 1, 1, and 1; one sleeping in the water with its pharyngeal pouches inflated; six active in the water, alongside the floes on which the central groups of females lay. The group of six inactive males was made up of one adult and five subadult animals, two of which had much blood on the body and on the snow around them. The six active bulls were spaced 7 to 10 m apart, and in a 35-min period of observation, we saw them dive and surface again many times in the same place.

6 March 1972, 0900 to 1900 h, at Lat. 63°04′N, Long. 172°23′W.—By helicopter we located several large herds totalling

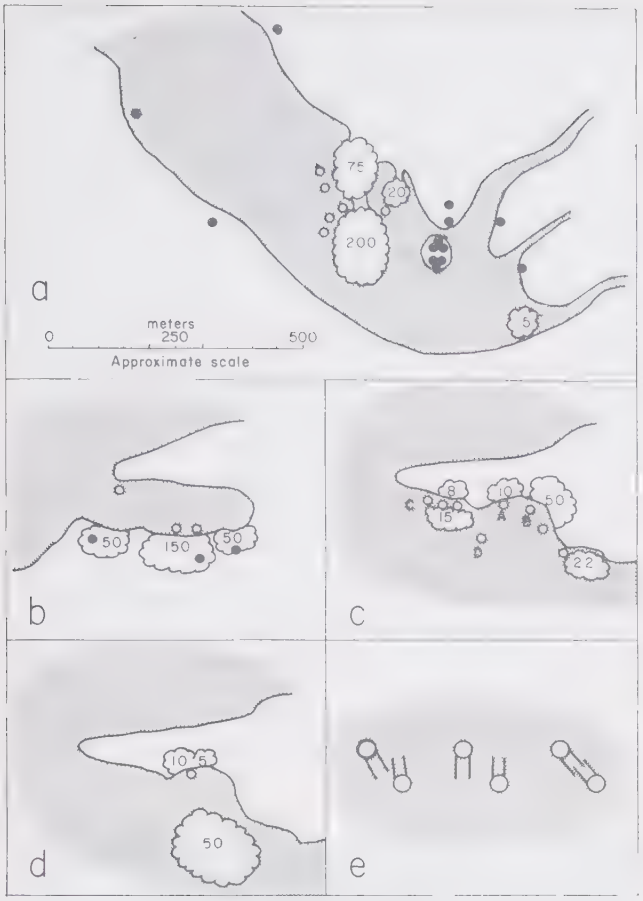


Figure 3.—Charts of the spatial arrangement of mixed herds of Pacific walruses observed in the north-central Bering Sea in March. The number of adult females and young is shown within each herd. Circles represent bulls that were active in the water (open) and those that were inactive or sleeping (solid): a) 4 March 1972, b) 8 March 1972, c) 9 March 1972, d) 10 March 1972, e) preliminary (tusk display) interactions of bulls A and B of 9 March. Open water and thin ice areas are shaded (see text for further description).

about 1,000 animals, most of which were adult females and young. A few adult bulls were present, some of them bloody about the head and leaving blood on the ice wherever they went. When the ship was moved to this position, we had four herds totalling about 500 animals within a 3 km radius. Nearly all were in the water, alternately diving and surfacing in remarkable synchrony and apparently feeding. Only one animal, an adult bull, was on the ice, sleeping, and he remained there throughout the daylight hours. One group of about 50 animals slept in the water near the ship for more than 2 h in the afternoon, before moving on. These were mainly females and young, but with them was one adult bull that was active the whole time, alternately diving and surfacing at 2- to 3-min intervals, in the midst of and about the periphery of the group.

7 March 1972, 0655 to 1900 h, at Lat. 63°00′N, Long. 172°04′W.—At daybreak, we sighted steam rising from three herds about 7 km from the ship and moved to that area for observation. All herds were in the water, evidently feeding, and these appeared to be entirely adult females and their young. Several single bulls were sleeping on the ice nearby. Between 0820 and 0920 h, nine other bulls hauled out nearby, two of them with blood streaming from superficial wounds. Except for two groups of two each, these were all single males which lay separately, about 50 to 100 m apart. Nearly all of these bulls remained in place throughout the daylight hours, whereas the herds of females were continuously moving. In late afternoon, one group of about 250 females and young hauled out to rest on a large floe about 1.5 km from the ship, in an area where we had seen one or two bulls sleeping previously. This group was still there at nightfall.

8 March 1972, 0700 to 1900 h, at Lat. 63°00′N, Long. 172°12′W.—The ship drifted slowly westward with the ice overnight and, at daybreak, was in the same position relative to the floe on which the herd had hauled out the previous afternoon. The resting herd of females and young was still in the same place, but most of the single bulls that we had seen the previous day were no longer on the ice. We left the ship on foot and took a position a few meters downwind from the resting herd. We found it to be made up of three partly separated groups of about 50, 150, and 50 adult females and young, each of which had in its midst one adult male (Fig. 3b). Those bulls slept soundly during our observations, except for occasional jostling of their closest neighbors for resting space. That is, we detected no activity that was even slightly suggestive of mating behavior, and certainly not indicative of a "beach master" role, as applied to otariids or elephant seals. We noted several times an emphatic "knock" sound, like that made by striking knuckles on wood, which seemed to come from the seaward edge of the groups. An occasional, short, loud whistle also came from the same location. We moved to the edge of the floe, a few meters from the perimeter of the largest group, where we observed three adult males in the water alongside the herd. These bulls were diving and surfacing at short intervals (1-3 min), each in a fixed location several meters from each other as in the foregoing observations. The dives, because of their brevity, did not appear to be feeding dives, which in our experience tend to be 5 to 10 min long at such depths (about 55 m). We observed these bulls for over an hour, in which their continuous activity contrasted greatly with that of the inactive males on the ice. The females seemed to pay little heed to the diving bulls, except when the latter surfaced with a burst of spray, wetting those nearest the edge of the floe. However, this only caused some jostling in the seaward edge of the herd.

By means of hydrophone and amplifier, we detected several underwater sounds, presumably made by the diving bulls. These sounds consisted of a series of "knocks" and "bell-like sounds" (see Schevill et al. 1966), but their significance and that of the other sounds made at the surface was not apparent to us at the time.

9 March 1972, 1600 to 1900 h, at Lat. 62°44′N, Long. 172°02′W.—We located a group of approximately 95 animals in the water and 20 that were just in the process of hauling out onto the ice. By 1800 h, there were about 70 adult females and immature animals on the ice in three groups of 8, 10, and about 50; two other groups (15 and 22) of females and young remained in the water, apparently feeding. Eight bulls also were in the water, "stationed" about 7 to 10 m apart along the edge of the ice where the females and young lay (Fig. 3c). On one occasion, male A surfaced close alongside male B, and the two animals faced each other. They held their tusks horizontally, first obliquely to one another, then parallel, then directly (Fig. 3e). Immediately thereafter, male B (who was the larger animal and had the larger tusks) rose chest-high out of the water and rapidly struck A three or four times on the head and neck with powerful downward thrusts of his tusks. Both animals dove in unison, with much splashing and churning of the water, then surfaced again, whereupon B rose once more and struck A two or three more times. Swiftly, they both dove again, surfaced briefly in a

shower of spray, then down again, then up and rolling together violently at the surface, then down again and remained beneath the surface for about 2 min. After this, each surfaced at his own station. Earlier, we had noticed a similar encounter between males C and D near C's station, and this also ended with each withdrawing to his usual station. It was not clear from our viewpoint on the ship exactly what these bulls were doing when not engaged in such fights, except that each was remaining in virtually the same place and repeatedly diving and surfacing there, as we had seen in the previous instances.

On one occasion, a subadult or young adult female approached bull A and engaged in some facial contact. She then mounted the male's back in what appeared to be a "copulatory" position, with the male and female roles reversed. The two then dove in unison, arching high out of the water. They remained underwater for about 1 min, then surfaced (the male first) and engaged in further facial contacts; then the female mounted the male again. They dove in unison once more, rolled together for a minute or more at a shallow depth, then surfaced slightly separated. The female swam away and hauled out again with a nearby group. Another female engaged male A in the same kind of activity about 30 min later.

Once again, underwater listening revealed "knocks" and the "bell-like" sounds. The ship remained overnight in the same position relative to the herd, drifting slowly southeastward with the ice.

10 March 1972, 0700 to 1430 h, at Lat. 62°36′N, Long. 172°08′W.—At daybreak, about half of the herd observed the previous evening was still present. The central group of 10 females and 5 youngsters was still on the ice; about 50 others were in the water evidently engaged in feeding. One adult male was in the water near the group of 10 females on the ice (Fig. 3d); no other males were in sight. We left the ship at 0830 h and approached on foot to within 30 m of the animals. We remained there about 5 h. During that time, the animals did not vary their distribution or their activities notably. The adult females and immature animals in the water were continuously engaged in feeding dives, with 1.5- to 2-min ventilation rests at the surface between dives; we did not determine diving times because individuals were difficult to distinguish from each other. Those on the ice mostly slept the whole time, except for a "crèche" of 5 first- and second-year youngsters that were engaged in mutual play. The bull repeatedly dove and surfaced in virtually the same place alongside the 10 females for the entire 5 h, pausing for 7 to 32 s at the surface between dives (Fig. 4 upper). His average time spent underwater was 2 min 2 s; his average time at the surface between dives was 23 s (Ray and Watkins 1975). As the bull surfaced following each dive, he released a large volume of air just beneath the surface and emerged nearly to shoulder height in a massive eruption of air and water. Raising his tusks nearly to the horizontal he made a "knock" which was audible to us for a distance of at least 200 m. At the time of emitting the "knock," he opened and closed his mouth very swiftly, seemingly making the sound by percussion of the cheek teeth. He inhaled deeply, then lowered his head so that only his crown showed above the surface, and lay floating for a few seconds with one pharyngeal air sac inflated and his back exposed. He then raised his head high enough to exhale and inhale noisily through his mouth, followed by another "knock" as he lowered his head again below the surface. He raised his head thus from one to four times during each surface interval, and on the last of these he "knocked," emitted a short whistle through pursed lips (Fig. 5

Figure 4.—Upper: 10 March 1972, group of 10 females and young resting on ice (center), attended by one displaying bull (arrow) who has just surfaced from a dive. Other females and young engaged in feeding are in the water at left (G. C. Ray photo). Lower: 21 March 1972, bull A (center) in mating display adjacent to group of 20 females and young, in which were two sleeping bulls (F. H. Fay photo).

Figure 5.—10 March 1972, displaying bull. Upper: making terminal "whistle," just prior to dive. Lower: diving after surface display sequence. Note height to which hind flippers are raised out of the water (G. C. Ray photos).

upper), then immediately dove, arching his back and rear flippers high out of the water (Fig. 5 lower).

During each dive, we heard the same stereotyped series of underwater pulses and bell-sounds[12] as we had heard on 8 and 9 March, including a distinctive 7-pulse coda (Ray and Watkins 1975). This whole sequence of sounds (Fig. 6) was audible to us in air from our position on the ice and was monitored and recorded by hydrophone, as well. Comparable sequences of underwater pulses and bell-sounds of lesser intensity, apparently made by other bulls some distance away and not within our field of vision, were heard via the hydrophone. At 1400 h, we intentionally disturbed the animals by exposing ourselves to their view and moving to their windward side, whereupon all of the females and youngsters departed. However, the bull continued his displays at his station for about 10 min longer, before departing in the direction of the females. Two other bulls, not seen previously, drew close to the area, then headed in the same direction.

17 March 1972, 1000 to 1300 h, at Lat. 62°47′N, Long. 172°28′W.—We encountered a group of 49 animals in an area of heavy, continuous ice with very few holes or leads. On the ice were 45 adult females and young, arranged in three groups of 6, 15, and 24; four adult males were situated as shown in Figure 7a. Bull A was sleeping on the ice; bull B was sleeping in the water in a round hole about the same diameter as his body. The other two bulls were displaying in the water, as in the previous incidents. Each had one of

[12]In air, walruses sometimes chatter their teeth, like a rodent. We have observed that "knocks" also can be produced when the jaw is moved rapidly as in percussion of the teeth. Nevertheless, we suspect that the knocking sound is produced by some other means. Fay and Kibal'chich watched an adult male "knocking" at close range (3 m) on 21 March 1976 but did not detect any jaw motion; rather, the sounds seemed to come from deeper in the throat. Kibal'chich has observed that the bell-sound made by walruses in air occurs at the time of inflation of one of the pharyngeal air sacs, but this has not been the case in hundreds of Fay and Ray's observations, in which animals floating at the surface, head down, were making the sounds without apparently varying the volume of air in their inflated sac(s).

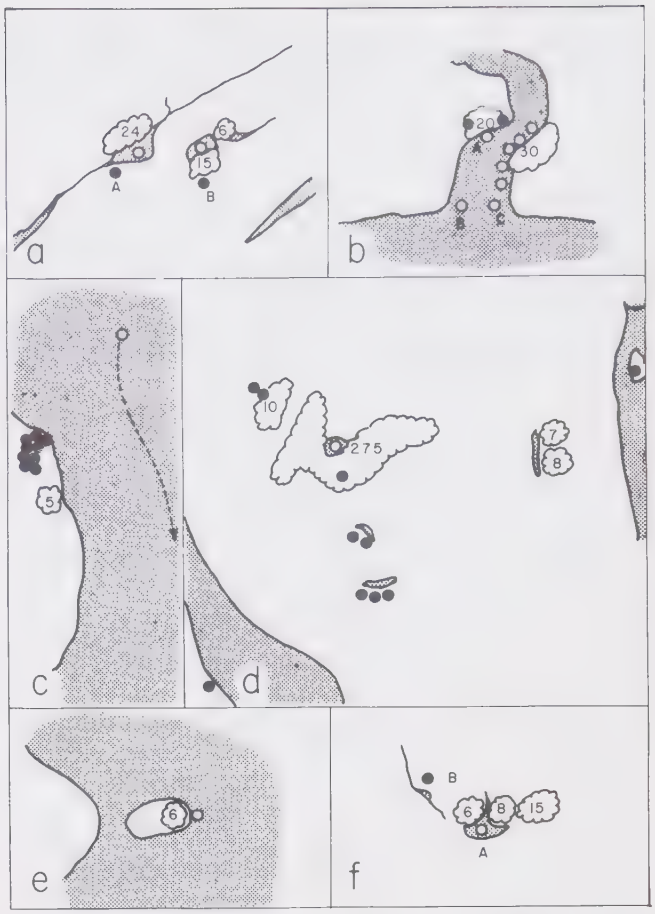


Figure 7.—Charts of the spatial arrangement of mixed herds of Pacific walruses observed in the north-central and southeastern Bering Sea during March and April. Symbols and scale are as in Figure 3: a) 17 March 1972, b) 21 March 1972, c) 21 March 1976, d) 3 April 1971, e) 5 April 1971, f) 10 April 1976 (see text for further description).

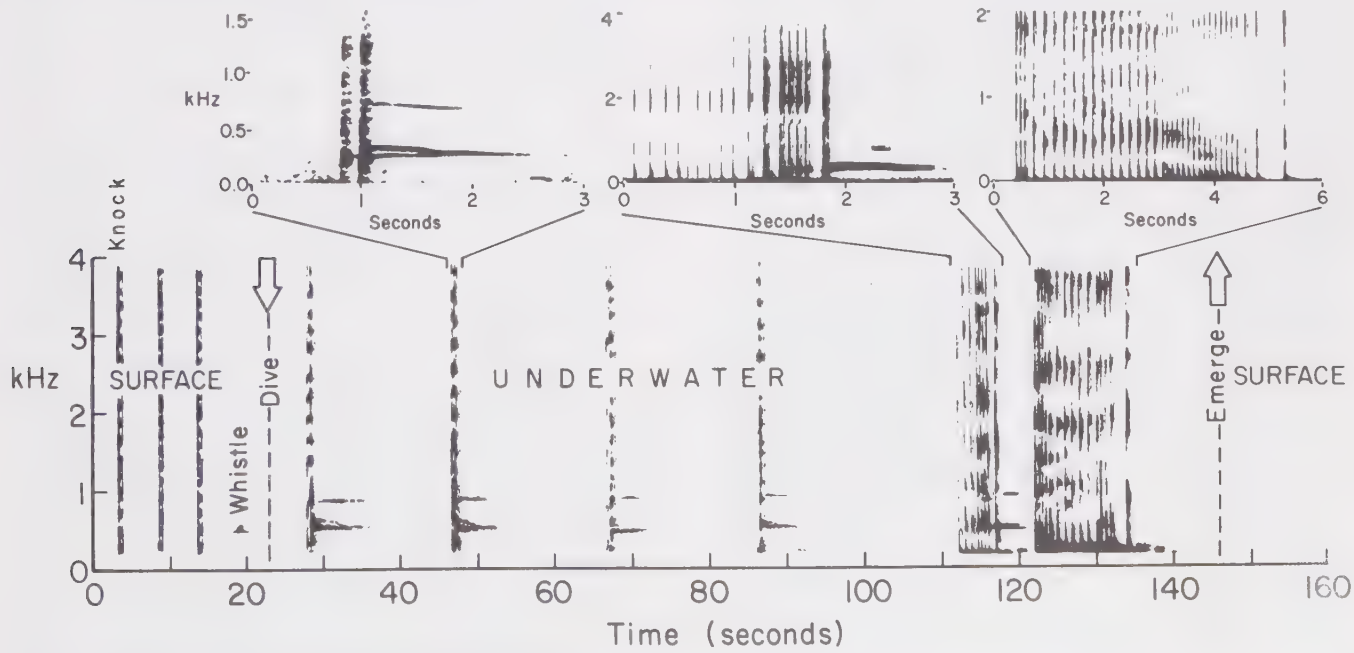


Figure 6.—Diagrammatic representation of a typical acoustical sequence during one display by an adult male. Insets are actual sonograms of parts of the underwater display (after Ray and Watkins 1975).

his pharyngeal pouches inflated while he was at the water's surface. We approached on foot and shot a female from each of the larger groups. This immediately frightened away all of the others except the displaying males, who continued their displays for a few minutes before moving in the direction of the departing females.

20 March 1976, about 1200 h, at Lat. 57°15′N, Long. 166°05′W.—We observed a group of four adults (2 males, 2 females) which lay in pairs, side by side on the ice, very close together but head-to-tail. A third male which swam to, and attempted to haul out on, the same floe was met with raised tusks but no overt aggression. He hauled out about 2 to 3 m apart from the group, whereupon they all laid down and were quiet.

21 March 1972, 0830 to 1300 h, at Lat. 61°27′N, Long. 174°24′W.—We encountered six herds on the ice and approached them on foot at 0830 h. There were about 250 animals in all, including mostly females and young on the ice and more than 10 adult males in the water. We concentrated our attention on two groups of 20 and 30 that were attended by 8 bulls (Fig. 7b). The group of 20 on the ice consisted of more than 10 adult and subadult females, about 8 juveniles (1 to 6 yr old), and 2 adult males. Nearly all of these animals had a coating of frost on their exposed body surfaces, indicating that they had been sleeping in the same position for several hours. The males in this group continued to sleep throughout the 4.5-h period of observation, as did most of the females and young. Only a few of the subadult and immature females were active, entering and leaving the water several times during the day. In the water near the ice edge was an adult bull (A) that was engaged in the same kind of dives and acoustical displays as the bulls observed earlier, though he did not stay as consistently in one place as the others had (Fig. 4 lower). The subadult and immature females that entered the water from this group often engaged in nose-to-nose and other facial contacts with this bull and occasionally dove with him, but we saw no copulation. A second bull (B), which at first stayed some 50 m away, later moved toward A's station. However, he did not come closer to A than about 10 m, nor did he engage in the display routine or elicit any evident response from bull A or from the young females. Subsequently, bull B returned to his former place, where he remained at the surface, making "bell" sounds with head submerged for about 1 h before moving out of view. At 1200, a third bull (C) appeared about 50 m away from A, but did not approach any closer. This animal did not engage in the same display sequence as the others, though he did dive occasionally and could have been making underwater sounds.

The larger group of about 30 animals also was frost-covered and consisted of adult and subadult females and immature animals of both sexes. There were no adult males in this group. However, three very large bulls, spaced about 5 m apart in the water along the edge of the floe, were continuously engaged in display routines all day; two other, smaller bulls in the water at one end of the group, displayed irregularly. The one most distant from the females was least active and, for an hour, simply floated at the surface emitting "bell" sounds, like bull B. A few of the youngest adult or subadult females in the resting group went into the water and actively engaged the bulls in nose-to-nose and other facial contacts. On several occasions, a female "mounted" a bull, and they participated together in considerable surface and subsurface rolling and splashing. We felt that copulation could have been taking place during these encounters, but we could not identify any copulations with certainty from our position.

21 March 1976, 0800 to 1300 h, at Lat. 56°45′N, Long. 166°00′W.—We observed a group of 5 adult females and young resting on ice and a group of 9 bulls and 1 juvenile male also on the ice about 8 m away from the first group (Fig. 7c). One bull was in the water about 0.5 km away but apparently was feeding, not displaying, since his dives were long (9-10 min) and he made no surface or underwater sounds. The group of females and young, after about 2 h of our observation, moved along the ice and joined the males, but other than some jostling for position, there was no interaction between the groups. We heard a few knocks and an occasional bell sound made by one or more of the bulls on the ice. We heard no underwater sounds by hydrophone.

3 April 1971, 1200 to 1800 h, at Lat. 61°52′N, Long. 171°45′W.—We encountered a congregation of some 300 animals, nearly all of which were asleep on the ice. Approaching on foot, we found them to be in several groups, the largest containing about 275 females and young and one centrally located, sleeping bull (Fig. 7d). Nearby was a smaller group of about 10 females and 2 adult bulls, also sleeping. Farther away were two groups of 7 and 8 pregnant (near-term) females, and scattered in groups of 1, 1, 2, and 3 within 1 km of the large central group were 7 adult and subadult bulls, also sleeping on the ice. A few animals were in the water near the largest group, and at least one of those was a displaying bull. No other bulls were sighted in the water.

5 April 1971, 1700 h, at Lat. 61°20′N, Long. 173°55′W.—We saw another group of 6 females and young on ice, attended by a large bull who was displaying alongside in the water (Fig. 7e).

10 April 1976, 1200 h, at Lat. 57°30′N, Long. 165°40′W.—We sighted three groups of 6, 8, and 15 females and young on adjacent floes. One bull (A) was displaying in the water between the two smaller groups; another bull (B) was on the ice about 10 m away (Fig. 7f). Bull B entered the water and approached A, displaying; he was promptly attacked by A, whereupon he withdrew and hauled out again in the same place. Underwater sounds, evidently from bull A, were like those made by the displaying bulls observed earlier.

DISCUSSION

All previous studies of reproduction in the Pacific walrus have been conducted entirely in late spring, summer, and autumn. Those studies have demonstrated clearly that implantation of the blastocyst takes place mainly in June and that the calf is born about 11 mo later, usually in May (Belopol'skii 1939; Freiman 1941; Nikulin 1941; Brooks 1954; Krylov footnote 5). However, the time and place of mating and the nature of breeding behavior have remained uncertain, for lack of specimens and observations during late autumn, winter, and early spring. Our specimens and behavioral observations have now provided enough information to indicate 1) that mating occurs mainly in winter rather than in spring, 2) that the population of females usually is split into two discrete groups (north-central and southeastern) during that period, and 3) that the social organization and behaviors of adults at that time are distinctively different from those in late spring, summer, and autumn.

Presuming that the mating season was in May and June, Belopol'skii (1939), Freiman (1941), Nikulin (1941), and Brooks (1954) speculated that small, loosely organized "harems" may be formed on the ice. They did not observe any such groups, however, and could only reiterate earlier analogies of sexual dimorphism and

gregariousness to support their views of an otariid-like system of polygyny. Neither have we seen any groups suggestive of an otariid-like "harem" structure during observations of hundreds of mixed herds in the Bering and Chukchi Seas in late April to early September. That is, in no case did any bull appear to be dominating a group of females or defending a territory; rather, the bulls usually were sleeping or jostling for resting space on the ice, or simply swimming or feeding in the water. In that period, the majority of males stay in all-male groups, some of which are very large (hundreds or even thousands). Many of these remain in the Bering Sea throughout the summer, while virtually all of the females and young migrate northward into the Chukchi Sea. We often have seen and heard subadult males in such all-male groups "displaying" to each other, as well as to mature males (Miller 1975:595-597). In those cases, the young animals' displays were "incomplete" and nonstereotyped; that is, they used only fragments of the full, stereotyped array of sounds and actions that characterize the displays of mature bulls in winter.

Conversely, we have observed that, in winter, most of the mature bulls occur singly and that they tend to follow and closely attend the herds of females. When the females are resting either in the water or on the ice, these bulls engage in ritualized visual and acoustical displays in the water near them. We believe that those displays function both as advertisement of the male's sexual readiness and as reinforcement of a dominance hierarchy among competitive males. Our observations indicate that, when bulls are engaged in this activity, they maintain an individual distance of no less than 5 to 10 m; any closer intrusion is met by threat, followed by fighting. We have never seen aggression of such intensity nor the association of displaying bulls with herds of females in any other season of the year.

For the most part, the subadult and juvenile males seem to remain outside the areas where the females and adult males congregate in winter. These younger males associate in small groups (2 to 20), some of which also include one adult male. They tend to become sexually active later in the season than do the older males, which would seem to be advantageous as protection from direct competition with their elders. We often have seen subadult males associated with females later in the spring and summer, after the adult males are no longer in rut and have formed all-male herds. If these younger bulls play a significant role in reproduction, it may be to fertilize cows that come into estrus after the main mating season.

In March, adult female/male interactions suggestive of precopulatory play occasionally took place when a female entered the water and swam to a displaying male. These interactions were brief (up to 3 min), and most of the activity took place underwater. Presumably copulation ordinarily occurs there (Scheffer and Kenyon 1963). About 80% of copulations by walruses in captivity take place in the water.[13]

Apart from these observations, we feel that the evidence for polygyny is compelling on several counts. First, we have observed that females outnumber males by about 10 to 1 in the wintering groups, and that the number of bulls attending a herd of cows seems to vary with its size, suggesting that there is some "optimal" sex ratio. There seemed always to be a few "extra" bulls, however, not far from each herd of females. At times, all of the bulls seemed to be resting on the ice, while the females and young were feeding. Because the older bulls tend to come into rut earliest, we suppose that there is a succession of progressively younger bulls in the mating areas as the seasons advance from winter to spring.

Second, Ralls (1977) has pointed out the high predictability in mammals between polygyny and sexual size dimorphism. Adult male Pacific walruses are about 20% longer and 50% heavier than adult females; further, they have larger tusks, much thicker, lumpy skin on the neck and shoulders, and are appreciably paler in color than the females (Fay 1982). Body and tusk size of males seem to be the principal determinants of social dominance (Miller 1975). Immature males tend to resemble the females in size, coloration, and smooth skin. The degree of sexual dimorphism is appreciably less than it is in most other polygynous pinnipeds, which suggests that the walrus's social organization is not as rigid, and that the feedback mechanism favoring dimorphism is not as strong as it is, for example, in the otariids (Bartholomew 1970).

Third, the maturing of the sexes at widely different ages generally is a corollary of polygyny, provided that all individuals of the sex which matures early are to breed (Wiley 1978). In all pinnipeds, the females apparently become capable of breeding a year to two earlier than the males (Harrison 1969), but by no means are all of them polygynous. The few that are known to be polygynous show an additional, distinctive feature of development that is a more conclusive corollary: Secondary acceleration of growth in the males (Laws 1959). While the males of polygynous species become physiologically capable of breeding not long after the females, they are unable to secure positions in the breeding structure until they have undergone this secondary, postpubertal growth and have reached a competitively large size, several years later. Male walruses, like the otariids and *Mirounga*, also undergo secondary growth, reaching their full adult size about 15 yr of age, some 5 to 6 yr after they become fertile and 7 to 8 yr after the females begin to breed (Fay 1982).

Each of these observations strongly indicates polygynous social organization, with inter-male competition for access to estrous females, but not necessarily the same kind of organization as that of the other polygynous pinnipeds. It clearly differs from the latter in four major respects: First, there is no discernable limit to the amount of breeding space available. The winter pack ice of the Bering Sea approaches 1 million km^2 in most years, and at least a third of it is inhabitable by walruses (Burns et al. footnote 11). Second, the winter pack ice is continually moving (mainly from north to south), and there is no fixed location within it to which the breeding adults can return each year, other than in very broad, general terms. They do seem to congregate with reasonable regularity within the two large areas shown in Figure 2, but the variations from year to year in extent and quality of the ice preclude site tenacity on a finer scale and, occasionally, preclude even the use of one or both of those areas. Third, the females do not congregate for calving just prior to the mating season. Birth of the calves takes place some months later, during the northward migration. Fourth, males on the ice with the females do not engage the females or other males in any behaviors that seem related to mating or defense of breeding territory. For the most part, they simply sleep, paying no heed to either the females around them or the displaying males in the water. Only the bulls in the water are aggressive toward each other and attentive to the presence and actions of the females.

Thus, the circumstances under which walruses mate are quite different from those of other polygynous pinnipeds, and this has been the strongest basis for argument in the past against polygyny in walruses. For example, Bartholomew (1970) dismissed the possibility of a polygynous system being maintained by a species that copulates in the water, since the greater mobility of pinnipeds there

[13]E. D. Asper, Curator of Mammals and Birds, Marineland, Orlando, FL 32809, pers. commun. August 1974.

than on land excludes the establishment of stable territories. Stirling (1975) felt that pack ice was unsuitable for organized polygyny because of 1) unlimited space for haulouts and 2) the instability of the ice itself, which is continually in motion. We suggest that the walrus is an exception. In this case, the "territory" seems to be more a matter of a 3-dimensional "individual space" around the male, in which acoustic displays reinforce the dominance established by body and tusk size and by fighting. The inherent gregariousness of the females, evidently irrespective of any influence by the males, assures unity of the breeding group, even in a habitat that is in motion and constantly changing.

The mating system implied by our observations is somewhat suggestive of a lek in that 1) the dominant males display before the females in a traditional location (albeit a very large and general one), 2) the subdominant males take peripheral positions, outside the "arena," and 3) the female appears to take the active role in consorting with the male of her choice within the arena (Wiley 1978). However, it does not seem to conform to the lek criterion of a place where males congregate to attract and court females, who come there just for mating (Wilson 1975). Rather, the females seem to congregate in the two large areas in winter more because of suitable ice conditions than for mating per se, and the males simply go there to engage them. Because the displaying males appear to control access to the females by defending their individual spaces alongside them, the social arrangement could be construed as a form of "female defense polygyny" in which the gregariousness of the females makes possible the monopolization of each herd by one or a few males (Bradbury *in* Kolata 1975; Emlen and Oring 1977). The fact that males continued to display after the females had left suggests that a male's "control" over a given herd is very temporary, perhaps lasting only for the period (24-48 h) when the females are resting between feeding bouts.

From what we know of it now, the mating system of the walrus seems most similar among pinnipeds to that of the northern elephant seal, as described by Le Boeuf and Peterson (1969), though it differs in some essential points, presumably because of its occurrence in the moving pack ice, rather than onshore.

ACKNOWLEDGMENTS

Our work was made possible by support from several sources over a period of many years. Fay's participation was sponsored in part by the Arctic Institute of North America, with approval and financial support of the Office of Naval Research under contract Nonr 1138 (01) subcontracts ONR-77 and 91; in part by the Alaska Sea Grant Program, supported by NOAA Office of Sea Grant, Department of Commerce, under grants GH-83, I-36109, and 04-3-158-41; and in conjunction with studies supported by the Bureau of Land Management through interagency agreement with the National Oceanic and Atmospheric Administration, under which a multiyear program responding to the needs of petroleum development of the Alaskan continental shelf managed by the Outer Continental Shelf Environmental Assessment Program (OCSEAP) Office. Some support and facilities were provided also by the U.S. Department of Health and Welfare, Public Health Service, in connection with its Arctic Health Research Program, and by the Institute of Marine Science, University of Alaska-Fairbanks. Ray's participation was sponsored by contracts to The Johns Hopkins University from the Office of Naval Research (Oceanic Biology), under contract N00014-75-C-0701, the National Aeronautics and Space Administration, under contract NAS2-9300, and the National Geographic Society. Kibal'chich's work was supported by the Soviet Ministry of Fisheries.

Logistical support was provided us additionally by the U.S. Department of the Interior, Fish and Wildlife Service, during two aerial surveys; by the U.S. Department of Transportation, Coast Guard, during the Arctic Winter West operations in 1971 and 1972 and Arctic Summer West of 1977, and by the Soviet Ministry of Fisheries, under agreement between the USA and USSR for Cooperation in the Field of Environmental Protection.

We gratefully acknowledge also the assistance of several colleagues who provided unpublished materials and aided us in gathering our data, namely John J. Burns of the Alaska Department of Fish and Game, Karl W. Kenyon and James A. Estes of the U.S. Fish and Wildlife Service, William A. Watkins of Woods Hole Oceanographic Institution, Donald H. Borchert of the Institute of Arctic Biology, University of Alaska, and our former students Howard M. Ferren, Edward H. Miller, Peter D. Shaughnessy, and Steven D. Sult. We have benefited also from the comments of Charles A. Repenning, Douglas Wartzok, Edward H. Miller, Burney J. Le Boeuf, and Ian Stirling on earlier drafts of the manuscript.

LITERATURE CITED

ALLEN, J. A.
1880. History of North American pinnipeds, a monograph of the walruses, sea-lions, sea-bears and seals of North America. U.S. Geol. Geog. Surv. Terr., Misc. Publ. 12, 785 p.

ASDELL, S. A.
1964. Patterns of mammalian reproduction. 2d ed. Comstock, Ithaca, N.Y., 670 p.

BARTHOLOMEW, G. A.
1970. A model for the evolution of pinniped polygyny. Evolution 24:546-559.

BELOPOL'SKII, L. O.
1939. On the migrations and ecology of reproduction of the Pacific walrus (*Odobaenus rosmarus divergens* Illiger). Zool. Zh. 18:762-774.

BERTRAM, G. C. L.
1940. The biology of the Weddell and crabeater seals: With a study of the comparative behaviour of the Pinnipedia. Br. Graham Land Exped. Rep. 1:1-139.

BRAHAM, H. W., J. J. BURNS, G. A. FEDOSEEV, and B. D. KROGMAN.
1984. Habitat partitioning by ice-associated pinnipeds: Distribution and density of seals and walruses in the Bering Sea, April 1976. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12:25-47.

BROOKS, J. W.
1954. A contribution to the life history and ecology of the Pacific walrus. M.S. Thesis, University of Alaska, Fairbanks, 103 p.

CARRICK, R., S. E. SCORDAS, and S. E. INGHAM.
1962. Studies on the southern elephant seal, *Mirounga leonina* (L.). IV. Breeding and development. C.S.I.R.O. Wildl. Res. 7:161-197.

CHAPMAN, D. G.
1964. A critical study of Pribilof fur seal population estimates. U.S. Fish Wildl. Serv., Fish. Bull. 63:657-669.

CHAPSKII, K. K.
1936. The walrus of the Kara Sea. Tr. Svesoyuz. Arkt. Inst. 67:1-124.

EMLEN, S. T., and L. W. ORING.
1977. Ecology, sexual selection, and the evolution of mating systems. Science (Wash., D.C.) 197:215-223.

FAY, F. H.
1955. The Pacific walrus: Spatial ecology, life history, and population. Ph.D. Thesis, Univ. British Columbia, Vancouver, B.C., Canada, 171 p.
1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North Am. Fauna 74, 279 p. U.S. Fish Wildl. Serv., Washington, D.C.

FREIMAN, S. J.
1941. Materials on the biology of the Chukchi walrus. Izv. TINRO 20:3-20.

GLUCKSMANN, A.
1974. Sexual dimorphism in mammals. Biol. Rev. Camb. Philos. Soc. 49:423-475.

GOL'TSEV, V. N.
1968. Dynamics of coastal herds of walruses in connection with their distribution and numbers. *In* V. A. Arsen'ev and K. I. Panin (editors), Pinnipeds of the northern part of the Pacific Ocean, p. 205-215. Pischevaya Promyshlennost', Moscow.

HARRISON, R. J.
1969. Reproduction and reproductive organs. *In* H. T. Andersen (editor), The biology of marine mammals, p. 253-348. Acad. Press, N.Y.

JOHNSON, A. M.
1968. Annual mortality of territorial male fur seals and its management significance. J. Wildl. Manage. 32:94-99.

KOLATA, G. B.
1975. Sociobiology (II): The evolution of social systems. Science (Wash., D.C.) 187:156-157.

KRYLOV, V. I.
1962. Rates of reproduction of the Pacific walrus. Zool. Zh. 41:116-120.
1965. Determination of age, rate of growth, and analysis of the age structure of the harvest of Pacific walruses. *In* E. N. Pavlovskii, B. A. Zenkovich, S. E. Kleinenberg, and K. K. Chapskii (editors), Marine mammals, p. 201-211. Nauka, Moscow.
1968. Present condition of Pacific walrus stocks and prospects of their rational exploitation. *In* V. A. Arsen'ev and K. I. Panin (editors), Pinnipeds of the northern part of the Pacific Ocean, p. 189-204. Pischevaya Promyshlennost', Moscow.
1969. The period of mating and calving of the Pacific walrus. *In* V. A. Arsen'ev, B. A. Zenkovich, and K. K. Chapskii (editors), Marine mammals, p. 275-285. Nauka, Moscow.

LAWS, R. M.
1959. Accelerated growth in seals, with special reference to the Phocidae. Nor. Hvalfangst-Tidende 48:425-452.

Le BOEUF, B. J.
1974. Male-male competition and reproductive success in elephant seals. Am. Zool. 14:163-176.

Le BOEUF, B. J., and R. S. PETERSON.
1969. Social status and mating activity in elephant seals. Science (Wash., D.C.) 163:91-93.

MANSFIELD, A. W.
1958. The biology of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus), in the eastern Canadian Arctic. Ph.D. Thesis, McGill University, Montreal, PQ, Canada, 146 p.

MILLER, E. H.
1975. Walrus ethology. I. The social role of tusks and applications of multidimensional scaling. Can. J. Zool. 53:590-613.

NIKULIN, P. G.
1941. The Chukchi walrus. Izv. TINRO 20:21-59.

NUTTING, C. C.
1891. Some of the causes and results of polygamy among the Pinnipedia. Am. Nat. 25:103-112.

RALLS, K.
1977. Sexual dimorphism in mammals; Avian models and unanswered questions. Am. Nat. 111:917-938.

RALLS, K., R. L. BROWNELL, Jr., and J. BALLOU.
1980. Differential mortality by sex and age in mammals, with specific reference to the sperm whale. Rep. Int. Whaling Comm. (Spec. issue 2) 1980:233-243.

RAY, G. C., and W. A. WATKINS.
1975. Social function of underwater sounds in the walrus *Odobenus rosmarus*. *In* K. Ronald and A. W. Mansfield (editors), Biology of the seal. Proceedings of a symposium held in Guelph 14-17 August 1972. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169:524-526.

ROPPEL, A. Y., and S. P. DAVEY.
1965. Evolution of fur seal management on the Pribilof Islands. J. Wildl. Manage. 29:448-463.

SCHEFFER, V. B., and K. W. KENYON.
1963. Baculum size in pinnipeds. Z. Säugetierkd. 28:38-41.

SCHEVILL, W. E., W. A. WATKINS, and G. C. RAY.
1966. Analysis of underwater *Odobenus* calls with remarks on the development and function of the pharyngeal pouches. Zoologica (N.Y.) 51:103-111.

STIRLING, I.
1975. Factors affecting the evolution of social behaviour in the Pinnipedia. *In* K. Ronald and A. W. Mansfield (editors), Biology of the seal. Proceedings of a symposium held in Guelph 14-17 August 1972. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 169:205-212.

TRIVERS, R. L.
1972. Parental investment and sexual selection. *In* B. Campbell (editor), Sexual selection and descent of man, p. 136-179. Harvard Univ. Press, Cambridge, Mass.

WILEY, R. H., Jr.
1978. The lek mating system of the sage grouse. Sci. Am. 238(5):114-125.

WILSON, E. O.
1975. Sociobiology: The new synthesis. Harvard Univ. Press, Cambridge, Mass., 695 p.

A List of American and Soviet Institutions Possessing Collections of Osteological Specimens from Pinnipeds and Sea Otters

LARRY J. HANSEN,[1] WILLIAM F. PERRIN,[1] ANATOLI S. SOKOLOV,[2] and JAMES G. MEAD[3]

ABSTRACT

Because different populations of the same species of pinnipeds and sea otters often have different populational parameters and histories of exploitation, modern conservation policy calls for identification of such management units below the specific level. To do so often requires analysis of large numbers of specimens from a morphological aspect, particularly by study of skeletal materials. By mutual agreement, to assist Soviet and American researchers in locating major sources of osteological specimens, we have compiled a list of the collections in the USA and USSR. Some 13,000 specimens of pinnipeds and 1,200 of sea otters, in 70 institutions, are recorded.

РЕЗЮМЕ

Разные популяции одного вида ластоногих, а также калана часто имеют разные параметры запасов и историю промысла. По этим причинам с позиций современной стратегии охраны необходимо идентифицировать такие популяции внутри вида.

В связи с этим зачастую требуется анализ большого количества морфологического материала, особенно по остеологии. По взаимному соглашению в целях окозания помощи американским и советским исследователям в определении местонахождения остеологического материала составлен настоящий список коллекций в США и СССР. Зафиксировано около 13000 экземпляров по ластоногим и 1200 по каланам в 70 учреждениях обеих стран.

INTRODUCTION

A major emphasis in modern conservation of marine mammals is on management by population or stock, because different populations of the same species quite often have different histories of exploitation and different levels of natural mortality and reproduction. A sound management policy for one population is not necessarily applicable to another population of the same species. For that reason, the International Whaling Commission and other management bodies, national as well as international, have increasingly moved to management on a stock-by-stock basis.

For many, if not most, marine mammals, populational variation and subdivision within the species are very poorly known or understood. The reasons for this are that 1) the decision for or against subdivision below the species level is based on morphology (osteology, coloration, body size and shape, etc.), and 2) morphological differences at that level are not absolute and require rigorous analysis of large numbers of specimens. Thus, modern management relies on the availability of large numbers of specimens. Unfortunately, marine mammal specimens are difficult and expensive to collect, process, and store. Consequently, most museums and other repositories possess only synoptic collections, or at best, a few dozen specimens of one or two species. For that reason, one usually must examine the specimens in many collections before reaching a conclusion on whether a particular subdivision of a species is justified. Before a collection can be used, of course, one must know what is in it; it must be cataloged and documented in a readily accessible publication or report.

Because of growing Soviet-American collaboration in research and management programs for marine mammals of mutual interest, the US-USSR Marine Mammal Project meetings in La Jolla, USA, in 1977 and in Ulan Ude, USSR, in 1978 endorsed the concept of cataloging world collections of marine mammal osteological specimens and agreed to assist and expand an existing cataloging effort by the U.S. National Museum of Natural History. This program has been underway for several years, with many major collections in the United States and Europe already documented. Collections in the Soviet Union have been included very recently and on a small scale. As the first step in a comprehensive cataloging program, specialists in the United States and the Soviet Union agreed to compile and exchange lists of collections which contain marine mammal specimens. The present list was compiled from that exchange.

METHODS

A total of 151 institutions, including universities, colleges, museums, government agencies, and oceanaria were surveyed. A list of institutions with marine mammal specimens compiled by Mead in 1973 served as a starting point for this survey. Other collections were located by reviewing catalogs of museums and educational institutions and published lists (Anderson et al. 1963:

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, USA.

[2]Academy of Sciences of USSR, Zoological Institute, Leningrad, USSR.

[3]Division of Mammals, National Museum of Natural History, Washington, DC 20560, USA.

Katz and Katz 1965; Choate and Genoways 1975; Podolsky 1975; Wolman 1978[4]). Each institution was contacted first by telephone. If the institution had marine mammal osteological specimens (a speciman may be anything from a single bone to a complete skeleton) an estimate of the number of specimens was obtained and a checklist questionnaire was mailed to the institution in order to obtain a more detailed inventory of the collection. Eighty-five percent of the questionnaires were returned.

RESULTS

Of the institutions surveyed, 70 reported pinniped osteological specimens (Table 1), and 81 did not. Six institutions reported only total numbers of marine mammal specimens.

Of the approximately 17,300 marine mammal specimens located, about 75% were pinnipeds and 7% were sea otters; the rest were cetaceans and sirenians. As an early form of the questionnaire included only cetaceans, pinnipeds, and sirenians,[5] the numbers indicated for sea otters probably are low. The U.S. National Museum of Natural History has the largest collection of pinnipeds, totaling about 2,500 specimens; the largest collection (about 1,400 specimens) in the USSR is in the Zoological Institute of the Academy of Sciences in Leningrad.

LITERATURE CITED

ANDERSON, S., J. K. DOUTT, and J. S. FINDLEY.
1963. Collections of mammals in North America. J. Mammal. 44:471-500.

CHOATE, J. R., and H. H. GENOWAYS.
1975. Collections of recent mammals in North America. J. Mammal. 56:452-502.

KATZ, H., and M. KATZ.
1965. Museums, U.S.A.; a history and guide. Doubleday, Garden City, N.Y., 395 p.

PODOLSKY, A.
1975. Education directory, higher education. U.S. Gov. Print. Off., Wash., D.C., 575 p.

[4]Wolman, A. A. 1978. International marine mammal scientists directory—1978. Processed rep., 81 p. National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[5]A list of cetacean and sirenian specimens in American and Soviet collections will be presented in Volume 2 of this publication series.

Table 1.—Institutions in USA and USSR possessing pinniped and sea otter osteological specimens, as of January 1979, based on survey.

Name of institution	No. of specimens: Pinnipeds	No. of specimens: Sea otters	Contact
Alaska Dep. Fish & Game Subport Bldg. Juneau, AK 99801	730	—	D. McKnight Game Research Chief
American Museum of Natural History Central Park W. at 79th St. New York, NY 10024	~750	—	S. Anderson Curator of Mammals
Bernice P. Bishop Museum P.O. Box 6037 Honolulu, HI 96818	15	—	A. C. Ziegler Vert. Zoologist
Calif. Academy of Sciences Dep. Birds & Mammals Golden Gate Park San Francisco, CA 94118	400	16	L. C. Binford Chairman
Calif. Polytechnic State Univ. Biological Sciences Dep. San Luis Obispo, CA 93409	43	119	A. I. Roest
Calif. State University Dep. Biology Hayward, CA 94542	9	1	H. Cogswell Curator
Calif. State University Dep. Biology 6101 East 7th Street Long Beach, CA 90804	17	3	Dr. Huckaby
Calif. State University Dep. Biology 5151 State University Dr. Los Angeles, CA 90032	6	—	
Calif. State University Dep. Biological Sciences 6000 J Street Sacramento, CA 95819	18	—	J. Tilley Museum Curator
Carnegie Museum 4400 Forbes Avenue Pittsburgh, PA 15213	463	—	Curator of Mammals
Charleston Museum 121 Rutledge Avenue Charleston, SC 29401	~4	1	A. Sanders Curator of Natural Sciences
Cornell University Bird & Mammal Museum, Bldg. 3 Ithaca, NY 14850	53	—	R. G. Bauer Curatorial Associate
Denver Museum of Natural History[1] City Park Denver, CO 80205	27	—	H. C. Wichers Curator of Mammals
Field Museum of Natural History Roosevelt Rd. at Lake Shore Dr. Chicago, IL 60605	189	—	S. Walchuk Division of Mammals
Florida State Museum University of Florida Gainesville, FL 32611	14	—	S. Humphrey
Harvard University Museum of Comparative Zoology Cambridge, MA 02138	566	—	E. Rutzmoser Curatorial Asst. of Mammals
Humboldt State University Dep. Zoology Arcata, CA 95521	81	—	R. Sullivan Vert. Zoology Museum
Los Angeles County Museum of Natural History 900 Exposition Blvd. Los Angeles, CA 90007	333	5	D. R. Patten
Louisiana State University Museum of Zoology Baton Rouge, LA 70803	1	—	J. P. O'Neal
Marineland of Florida Route 1, Box 122 St. Augustine, FL 32084	1	—	R. Jenkins

Michigan State University The Museum East Lansing, MI 48823	24	—	J. Matson
Monkshire Museum of Science Hanover, NH 03755	3	—	R. Chaffee
National Marine Fisheries Service La Jolla Laboratory P.O. Box 271 La Jolla, CA 92038	2	1	W. F. Perrin, L. J. Hansen
National Marine Fisheries Service Marine Mammal Division 7600 Sand Point Way, Bldg. 32 Seattle, WA 98115	271	3	C. Fiscus
National Museum of Natural History Division of Mammals Smithsonian Institution Washington, DC 20560	~2,500	500	J. G. Mead Curator of Marine Mammals
New England Aquarium Central Wharf Boston, MA 02110	15	1	L. Garibaldi Curator
New York State Museum Washington Avenue Albany, NY 12224	1	—	P. Connor
North Carolina State Museum P.O. Box 2281 Raleigh, NC 27611	3	—	D. Lee Curator of Mammals
North Carolina State University Dep. Zoology Raleigh, NC 27607	7	—	Dr. Barkaloo
Ohio Historical Society[1] Natural History Division Ohio Historical Center Columbus, OH 43211	3	—	C. W. Albrecht Curator of Natural History
Oklahoma State University Museum of Natural History Stillwater, OK 74074	10	2	B. Glass
Oregon Institute of Marine Biology Charleston, OR 97420	2	2	J. Hanna
Oregon State University Marine Science Center Newport, OR 97365	17	—	B. Mate
Peabody Museum of Natural History Yale University New Haven, CT 06520	66	—	J. Ostrom
Peabody Museum of Salem Salem, MA 01970	2	—	S. Pidugalls
Philadelphia Academy of Science 19th St. and Parkway Philadelphia, PA 19103	137	—	F. B. Gill
Princeton University Museum of Natural History Princeton, NJ 08540	15	—	D. Baird Geology Dep.
San Diego Natural History Museum P.O. Box 1390 San Diego, CA 92112	130	—	R. M. Chandler Curator of Birds & Mammals
San Jose State University 125 South Seventh Street San Jose, CA 95162	103	—	J. Vollenweider Museum of Birds & Mammals
Santa Barbara Museum of Natural History 2559 Puesta del Sol Road Santa Barbara, CA 93105	85	48	C. Woodhouse Head, Marine Mammal Program
Southern Illinois University Zoology Department Carbondale, IL 62901	4	2	E. C. Gallbreath
University of Alaska Museum University of Alaska Fairbanks, AK 99701	487	8	S. MacDonald
University of California Museum of Vertebrate Zoology 2593 Life Sciences Bldg. Berkeley, CA 94720	262	28	W. Z. Lidicker, Jr. Curator of Mammals
University of California Dep. Zoology Davis, CA 95616	17	—	M. Hildebrand
University of California School of Veterinary Medicine Davis, CA 95616	10	—	L. M. Julian
University of California Biology Dep., Dickey Collections Los Angeles, CA 90024	28	—	J. Miller Curator
University of California Santa Cruz, CA 95060	~10	—	T. Dohl
University of Colorado Museum Boulder, CO 80302	14	—	S. K. Wu Curator of Zoology
University of Connecticut Dep. Biological Sciences Storrs, CT 06268	10	—	R. Dubos
University of Kansas Museum of Natural History Lawrence, KS 66044	~12	~1	R. S. Hoffman Curator of Mammals
University of Miami School of Marine Sciences 4600 Rickenbacker Causeway Miami, FL 33149	4	—	J. Reynolds
University of Michigan Museum of Paleontology Ann Arbor, MI 48104	2	—	Dr. Smith
University of Michigan Museum of Zoology Ann Arbor, MI 48104	24	—	P. Myers
University of Missouri Museum of Zoology Columbia, MO 65201	60	—	Dr. Elder
University of Montana Dep. Zoology Missoula, MT 59801	19	—	
University of New Mexico Dep. Biology Albuquerque, NM 87106	10	—	J. Finley
University of Notre Dame Dep. Biology Notre Dame, IN 46556	1	—	
University of Oregon Museum of Natural History Eugene, OR 97403	17	2	E. Gustafson
University of Puget Sound Puget Sound Museum of Natural History Tacoma, WA 98416	374	34	E. Kritzman
University of Texas, Austin Texas Memorial Museum 2400 Trinity Austin, TX 78705	~6	—	R. Martin

University of Washington Burke Museum Seattle, WA 98195	53	—	J. Rozdilsky Zoology Div.
Virginia Polytechnic Institute and State University Dep. Biology Blacksburg, VA 24061	6	—	J. Crawford
Waikiki Aquarium 2777 Kalakaua Avenue Honolulu, HI 96815	1	—	L. Taylor
Washington State University Dep. Zoology Conner Zoology Museum Pullman, WA 99164	30	—	R. E. Johnson
Moscow State University Zoological Museum Moscow, USSR	1,124	0	O. L. Rossolimo I. R. Pavlinov
Academy of Sciences of USSR Zoological Institute Leningrad, USSR	1,426	261	I. M. Gromov
Atlantic Research Institute of Fisheries and Oceanography Kaliningrad, USSR	372	0	V. A. Zheglov G. V. Rezvov I. E. Filatov
Pacific Research Institute of Fisheries and Oceanography Vladivostok, USSR	379	195	G. M. Kosygin
Magadan Section Pacific Research Institute of Fisheries and Oceanography Magadan 685013, USSR	1,247	0	G. A. Fedoseev
Petropavlovsk Section Pacific Research Institute of Fisheries and Oceanography Petropavlovsk-Kamchatka, USSR	16	0	

[1]Status of collection as of 1973.

Guidelines for Contributors

CONTENTS OF MANUSCRIPT

First page. Give the title (as concise as possible) of the paper and the author's name, and footnote the author's affiliation, mailing address, and ZIP code.

Contents. Contains the text headings and abbreviated figure legends and table headings. Dots should follow each entry and page numbers should be omitted.

Abstract. Not to exceed one double-spaced page. Footnotes and literature citations do not belong in the abstract.

Text. See also Form of the Manuscript below. Follow the *U.S. Government Printing Office Style Manual,* 1973 edition. Fish names, follow the American Fisheries Society Special Publication No. 12, *A List of Common and Scientific Names of Fishes from the United States and Canada,* fourth edition, 1980. Use short, brief, informative headings in place of "Materials and Methods."

Text footnotes. Type on a separate sheet from the text. For unpublished or some processed material, give author, year, title of manuscript, number of pages, and where it is filed—agency and its location.

Personal communications. Cite name in text and footnote. Cite in footnote: John J. Jones, Fishery Biologist, Scripps Institution of Oceanography, La Jolla, CA 92037, pers. commun. 21 May 1977.

Figures. Should be self-explanatory, not requiring reference to the text. All figures should be cited consecutively in the text and their placement, where first mentioned, indicated in the left-hand margin of the manuscript page. Photographs and line drawings should be of "professional" quality—clear and balanced, and can be reduced to 42 pices for page width or to 20 picas for a single-column width, but no more than 57 picas high. Photographs and line drawings should be printed on glossy paper—sharply focused, good contrast. Label each figure. DO NOT SEND original figures to the Scientific Editor; NMFS Scientific Publications Office will request these if they are needed.

Tables. Each table should start on a separate page and should be self-explanatory, not requiring reference to the text. Headings should be short but amply descriptive. Use only horizontal rules. Number table footnotes consecutively across the page from left to right in Arabic numerals; and to avoid confusion with powers, place them to the *left* of the numerals. If the original tables are typed in our format and are clean and legible, these tables will be reproduced as they are. In the text all tables should be cited consecutively and their placement, where first mentioned, indicated in the left-hand margin of the manuscript page.

Acknowledgments. Place at the end of text. Give credit only to those who gave exceptional contributions and *not* to those whose contributions are part of their normal duties.

Literature cited. In text as: Smith and Jones (1977) or (Smith and Jones 1977); if more than one author, list according to years (e.g., Smith 1936; Jones et al 1975; Doe 1977). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited"; only the author's surname and initials are required in the author line. The author is responsible for the accuracy of the literature citations. Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations.* Format, see a recent Technical Report.

Abbreviations and symbols. Common ones, such as mm, m, g, ml, mg, °C (for Celsius), %, °/₀₀, etc., should be used. Abbreviate units of measures only when used with numerals; periods are rarely used in these abbreviations. But periods are used in et al., vs., e.g., i.e., Wash. (WA is used only with ZIP code), etc. Abbreviations are acceptable in tables and figures where there is lack of space.

Measurements. Should be given in metric units. Other equivalent units may be given in parentheses.

FORM OF THE MANUSCRIPT

Original of the manuscript should be typed double-spaced on white bond paper. Triple space above headings. Send good duplicated copies of manuscript rather than carbon copies. The sequence of the material should be:

FIRST PAGE
CONTENTS
ABSTRACT
TEXT
LITERATURE CITED
TEXT FOOTNOTES
APPENDIX
TABLES (provide headings, including "Table" and Arabic numeral, e.g., Table 1.—, Table 2.—, etc.)
LIST OF FIGURE LEGENDS (entire legend, including "Figure" and Arabic numeral, e.g., Figure 1.—, Figure 2.—, etc.)
FIGURES

ADDITIONAL INFORMATION

Send ribbon copy and two duplicated copies of the manuscript to:

Dr. William J. Richards, Scientific Editor
Southeast Fisheries Center Miami Laboratory
National Marine Fisheries Service, NOAA
75 Virginia Beach Drive
Miami, FL 33149

Copies. Fifty copies will be supplied to the senior author and 100 to his organization free of charge.

UNITED STATES
DEPARTMENT OF COMMERCE
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
NATIONAL MARINE FISHERIES SERVICE
SCIENTIFIC PUBLICATIONS OFFICE
7600 SAND POINT WAY N.E.
BIN C15700
SEATTLE, WA 98115
OFFICIAL BUSINESS

POSTAGE AND FEES PAID
U.S. DEPARTMENT OF COMMERCE
COM-210

THIRD CLASS
BULK RATE

U.S.MAIL

NOAA SCIENTIFIC AND TECHNICAL PUBLICATIONS

The National Oceanic and Atmospheric Administration was established as part of the Department of Commerce on October 3, 1970. The mission responsibilities of NOAA are to assess the socioeconomic impact of natural and technological changes in the environment and to monitor and predict the state of the solid Earth, the oceans and their living resources, the atmosphere, and the space environment of the Earth.

The major components of NOAA regularly produce various types of scientific and technical information in the following kinds of publications:

PROFESSIONAL PAPERS—Important definitive research results, major techniques, and special investigations.

CONTRACT AND GRANT REPORTS—Reports prepared by contractors or grantees under NOAA sponsorship.

ATLAS—Presentation of analyzed data generally in the form of maps showing distribution of rainfall, chemical and physical conditions of oceans and atmosphere, distribution of fishes and marine mammals, ionospheric conditions, etc.

TECHNICAL SERVICE PUBLICATIONS—Reports containing data, observations, instructions, etc. A partial listing includes data serials; prediction and outlook periodicals; technical manuals, training papers, planning reports, and information serials; and miscellaneous technical publications.

TECHNICAL REPORTS—Journal quality with extensive details, mathematical developments, or data listings.

TECHNICAL MEMORANDUMS—Reports of preliminary, partial, or negative research or technology results, interim instructions, and the like.

Information on availability of NOAA publications can be obtained from:

PUBLICATIONS SERVICES BRANCH (E/AI 13)
NATIONAL ENVIRONMENTAL SATELLITE, DATA, AND INFORMATION SERVICE
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
U.S. DEPARTMENT OF COMMERCE

3300 Whitehaven St.
Washington, DC 20235